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Effect of scale of measurement on estimation of genetic parameters

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EFFECT OF SCALE OF MEASUREMENT ON ESTIMATION OF GENETIC PARAMETERS

by

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I. INTRODUCTION

Estimates of phenotypic and genetic parameters are used in the solution of animal breeding problems. The validity of procedures used to obtain these estimates rests upon various assumptions which may be statistical or related to the biology and genetics of the species and traits concerned. There is no clear division, however, between the statistics and the biology since the choice of statistical tools depends upon the biological nature of the material under study. The statistical assumptions are largely those of the analysis of variance, including linear regression.

The phenotypic scale on which a trait is measured or expressed is directly involved in any assessment that might be made of the validity of these assumptions, biological or statistical. There is therefore a fundamental relation between phenotypic scales and the practical values which can be placed upon estimates of genetic parameters and consequent breeding plans.

In the present study, criteria used to assess the relative values of different phenotypic scales are considered and several transformations of scale and derived scales are investigated in relation to the estimation of heritability and genetic correlations from the resemblance between daughters and their dams. Large numbers of dairy records were available so that three important traits in dairy cattle were chosen to form the basis of the investigation. For much of the analysis, the records were grouped in order to make the

scales of measurement more amenable to transformation. However, the number of groups was kept as large as possible in order to minimize any loss of information due to the grouping process.

II. THE ASSUMPTIONS UNDERLYING THE ESTIMATIONS

The statistical assumptions underlying the estimation of heritability and genetic correlations are largely those of the analysis of variance. Since the solutions to the analysis of variance problem are based on the theory of "least squares", the assumptions are those of the Gauss-Markoff theorem. This theorem states that, given random variables which are observations Y_i, $i = 1, 2, \ldots, n$, such that

$$Y_i = E(Y_i) + e_i,$$

and $E(Y_i)$ is a linear function of unknown parameters,

$$E(e_i) = 0$$

$$E(e_i\, e_{i'}) = 0, \quad i \neq i',$$

and $E(e_i^2) = \sigma^2$ for all i,

then the method of least squares gives the best linear, unbiased estimate of any linear function of the parameters which can be estimated. The best estimate is taken to be the one having minimum variance. This theorem is discussed by Kempthorne (1952) who calls it simply the Markoff theorem.

The assumptions of the above are that the Y_i can truly be described by a model that is linear, that the errors (the e_i) have mean zero and are uncorrelated, and that the error variance is a constant for each value of the random variable (Y_i). These assumptions have been discussed in the classical paper of Eisenhart (1947).

A numerical description of the sample data can be given by the procedures of analysis of variance regardless of whether or not the

assumptions are true. However, in genetics, the main objective is normally to be able to make inferences about the properties of the population from which the data were drawn as a sample and, for such inference to be valid, the assumptions should hold true. For example, an estimate of heritability can be calculated from some data but, unless the data conform to the assumptions outlined above, little can be said with any degree of surety about the population parameter.

If it is desirable to make tests of significance and place reliability factors on estimates from linear models, it is necessary to completely specify the error distribution for all random variables. It is usual to assume normality for these distributions because this is most often biologically sensible and the normal distribution is well known. A linear function of normally distributed random variables is itself normally distributed and a normal distribution is completely specified by its first two moments. If the errors are mutually uncorrelated and are normally distributed then they are independent. Although the usual theory for tests of hypotheses requires normal distributions of errors, Cochran (1947) gives as the consenus of previous research that non-normality introduces no serious errors in the significance levels of the F test and two-tailed t test. Similarly, the effect on the estimation of standard errors and on the efficiency of estimation of "effects" is not likely to be great. It is suggested that extreme skewness of the distribution could be the greatest source of problems.

Heterogeneity among error variances can lead to considerable

losses in the efficiency of estimation of "effects" and in the sensitivity of tests of significance (Cochran, 1947). The problem can often be solved by using a weighted analysis of variance but this is seldom easy in practice. Tests for the equality of variances are known but do not share the insensitivity to general non-normality of the parent population possessed by the robust analysis of variance tests mentioned above (Box, 1953). Heterogeneity can arise out of non-normality, there often being a relation between the variance of an observation and its mean in non-normal populations (Cochran, 1947). Such cases may often be conveniently handled by transformation of scale. Non-additivity in the model may also produce heterogeneity among the error variances.

Anscombe and Tukey (1963) draw attention to the problem of differential diagnosis of any misbehavior in the data, it being difficult to separate the effects of outliers from those of non-normality (especially excessive skewness), from those caused by excessive variation in a part of the data, from those of certain types of non-additivity and from those of the dependence of the variance upon the mean. Action which minimizes the effects of one sort of misbehavior might lessen the effects of one or more of the others to a greater or lesser degree.

The validity of the model and of assumptions about the model generally rests upon biological considerations. Whether the model is biologically correct or not depends upon knowledge of the biology (genetics) of the traits and species involved. It is appropriate to

set up additive, linear models, each with the required error structure, but often the only evidence as to the fit of models to reality comes from whether or not the results obtained are in line with those expected as a result of experience gained in independent research or in practice. The conformation of the data to the model and assumptions can sometimes be assessed by examination of the "residuals" remaining after values for the components of the model have been determined (Anscombe and Tukey, 1963). Often the data can be made to conform to an appropriate model by suitable choice of scale or transformation of scale, the model can be changed, or the experimenter can discriminate among the individual observations by, for example, the rejection of outliers.

III. CRITERIA FOR SCALES OF MEASUREMENT

In quantitative genetic analysis, individuals and groups are described in terms of means and variances on some metric scale. The description of the data is valid only in terms of the scale on which a trait is measured and, as Mather (1949) has put it, "clearly the choice of an appropriate scale is the first step in the analysis of polygenic variation."

The first, and often the only, criterion used in the choice of scale is that of convenience. It is perhaps fortunate that many convenient scales have other desirable properties and are readily adaptable to chosen measuring systems. For example, it is both desirable for statistical purposes and also convenient that scales should regularly increase or decrease, meaning that successive units of the scale should be consistent with either an increasing or a decreasing expression of the trait being measured. Likewise it is desirable and convenient that scales be additive, each unit being exactly alike to each other unit on the scale.

It would seem to be good from a biological standpoint to use a scale which is close to the scale on which the genetic processes are acting, and this suggests the use of a scale giving maximum values to heritability. Such a scale should be most closely related to the genotypic scale. In genetic statistics, the assumption is usually made that the genotypic scale is primarily additive, but with deviations due to dominance and epistasis. If this is true, and the linear re-

gression of genotype on phenotype is to describe adequately the heritability of a trait, then the phenotypic scale should be as near additive as possible. To maximize the heritability of a trait, it is necessary to reduce the total phenotypic variance in proportion to the additive genetic variance by elimination of some of the non-additive genetic variance and interaction variances.

What is needed is some way of dealing with gene X gene interactions (dominance and epistasis) and genotype X environment interactions. Such interactions can be taken care of by the addition of terms to the model, but if they can be made to disappear by transformation of scale, the analysis and interpretation should be facilitated. Falconer (1960) has suggested that if effects are removed by transformation, the necessity to look for genetic causes of the phenomena is avoided. This approach seems rather too escapist, but the amounts of gene interaction removable by transformation will probably be small. Results from the mathematical treatment of epistasis by Horner et al. (1955) suggest that biases in the estimates of both additive genetic variance and level of dominance resulting from strictly multiplicative gene action are relatively small. However, the types of interaction which can be readily dealt with by transformation of scale, such as the multiplicative type, probably represent the least extreme deviations from a no-interaction model.

The problem of how to detect non-additivity and to characterize it still remains. Falconer (1960) points out the need for some in-

dependent criterion to justify a scale and the approach of Rae (1950) sets up the maximization of heritability as just such a criterion. It seems that by changing the phenotypic scale to maximize the heritability, some of the previously non-additive genetic proportion, if any, of the total phenotypic variance should be removed, and the genetic gain expected from mass selection increased. A scale found by this method is empirical and relates only to the set of data from which it is derived making general application to the analysis of other data hazardous. Even so, a great deal of uniformity exists among current estimates of parameters using different sets of data from the same species and trait. Consequently, some generality might be expected. The method of Rae (1950) is discussed in detail in section VIII.

Quantitative genetic theory postulates that a quantitative trait is determined by a large number of loci, at each of which two or more alleles are possible, and it is reasonable to suppose independence of many of these contributing units (Falconer, 1960; Kempthorne, 1957; Lush, 1945). Laplace's principle states that a variable compounded additively of many small, independent contributions shows an approximately normal distribution, irrespective of the natures of the frequency distributions of the separate components (Wright, 1952). This principle is demonstrated by the approximation to the normal of the binomial distribution as the size of the sample becomes large. The suggestion is that the genotypic expression of the trait is likely to be normally distributed, and this suggests the use of a scale on which the phenotypic expression of the trait is likewise normally distributed.

Many traits are normally distributed when an additive scale is used, but others are distorted, possible because of the effects of interactions.

The practical utility of the normal distribution can be seen best by consideration of selection theory. Given a normal population and the first two moments of the distribution, the selection intensities and the necessary genetic statistics, it is possible to predict the likely progress from selection, at least over a few generations assuming a linear response. It is also usual to assume, perhaps not very realistically, truncation selection. The prediction can be done both for single traits and for correlated traits, when the latter are from a multivariate normal distribution. The mathematical bases for such prediction have been given in detail by Cochran (1951). While the general results do not require specification of the normal distribution, it is necessary for prediction purposes to know the form of the distribution of the selection criterion and when this criterion does not follow the normal, it may be very difficult to make generalized predictions. If a normal distribution is assumed and expected gains are calculated, these may be in error if departures from normality are at all great, especially in the tails of the distribution. However, moderate departures may have little effect if selection is weak and the expected progress is small.

As mentioned in section II, the error variance may change with the mean and this may be due to non-normality of the distribution or to

lack of additivity in the true model. The scale of measurement has an important influence on the relation between variance and mean and a transformation may be required to obtain independence of the two parameters. A general procedure to find the form of such a transformation has been given by Bartlett (1947) and Kempthorne (1952). According to Bartlett (1947), a scale chosen to stabilize the variance will, as a rule, be one on which arithmetic averages will be efficient estimators of true mean levels, an important property, and the distribution of the trait on the transformed scale will be closer to normal.

It is most important that the scale for a trait be one on which real effects, both genetic and non-genetic, are additive, but it is difficult to determine a scale which achieves this property. It has been suggested by Kempthorne (1952) that, in general, the best procedure is to obtain a transformation which results in homogeneity of the error variance and to assume deviations from additivity on the transformed scale to be minimal.

It has already been indicated that transformations of scale can be made in order to make the data more closely conform to the assumptions necessary for valid analysis. It should be remembered however, that the results will be meaningless if they cannot be interpreted in a manner which makes biological sense. The statistical success of a transformation can be judged by the numerical value of some criterion, and Tukey (1957) has discussed ways in which an understanding can be reached of how such a criterion may vary over a whole family of transformations. Since there is evidence that analysis proceeds more easily

if effects are additive, if the error variance is stable, and if the distribution of errors is symmetric and if possible near normal, criteria can be set up to make it possible to judge the effectiveness of a transformation in bending the data to fit these requirements. One such criterion is that for non-additivity of Tukey (1949).

Falconer (1960), in his chapter on scale, has suggested that the best scale may be different for the same trait in different populations or for the genetic and environmental portions of the phenotype, and Mather (1949) has pointed out that a scale which is biologically representative or that reflects all genetic situations should not be expected. Most authors stress that no transformation can be expected to work perfectly and changes of scale should not be made without good reason. Transformations may well remove metrical biases arising from inadequate scales, but they may also obscure the description of some of the genetic properties of the population. The problem must be considered new for every trait in every population and, as Falconer (1960) points out, it is illusory to presume that every trait has its natural or correct scale.

IV. SOURCE OF DATA

The data for this study were obtained through routine milk and butterfat recording by the Dairy Herd Improvement Associations in the mid-western states of Iowa and Minnesota. These associations operate the production recording of dairy cattle data which is supervised by the extension services in each state in cooperation with the United States Department of Agriculture. Each association is a cooperative venture of a group of dairy farmers who hire a supervisor to visit each member farm once every month. The supervisor weighs and samples each cow's milk for the test day, conducts butterfat (and for some herds solids-not-fat) tests on the samples, and records other information relative to the productivity and economics of the cattle and the herd. The information is mailed to a processing center where it is put into a form suitable for the general use of association members. Central processing of dairy records began in the state of Utah in 1952, and Iowa State University established a center in 1958 to serve nine* mid-western states (Taylor, 1962).

The basic lactation data were standardized for length (305 days), age (mature equivalent), and number of milkings per day (twice-a-day milking). Multiplicative factors of the United States Department of Agriculture (Kendrick, 1955) were used for the standardizations.

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*Arkansas, Iowa, Kansas, Minnesota, Missouri, Nebraska, North Dakota, Oklahoma, and South Dakota

The lactation records came from Holstein cows most of which were in herds on central processing. Of the 5,209 daughter records actually used in later analyses, only 14 were of lactations initiated before 1958, and of the corresponding 5,209 dam records, 515 were of lactations so initiated. The Holstein breed was chosen because of its popularity and the consequent availability of large numbers of records. Of all records summarized in the 1964 summary of the Iowa Dairy Herd Improvement Associations, 76.4% were from Holstein cows, of which 29.1% were registered and 70.9% grade. The standardized lactation average of all these 34,532 cows was 438 lbs. of fat and 12,123 lbs. of milk containing 3.6% fat (Iowa State University, 1964).

A total of 65,449 complete first lactation records from cows freshening in 3,857 herds between 1945 and 1963, inclusive, were used. The average herd size in Iowa is comparatively small, the average size in 1963-64 being 32.2 cows. First lactation records only were selected for the sake of simplicity and to keep the sources of variation to a minimum. From a survey of the literature and from analysis of Holstein data similar to that used in the present study, Molinuevo and Lush (1964) have concluded that the first lactation record gives a somewhat more accurate estimate of the breeding value of a cow than the second or third record, while Freeman (1960) has suggested that, to some extent, different sets of genes influence milk and fat production in different lactations.

Each 305 day, mature equivalent, first lactation record was

deviated from its respective regressed, adjusted, herd-year-season average of all available records. The deviations were computed by W. R. Taylor following the methods detailed by Bereskin (1963) and the data became available to the present author in deviated form. In theory, the deviation of a cow's record from the average of her contemporaries accomplishes the removal of herd, year, and season of calving effects but, in practice, some residual variance due to these sources remains (Bereskin and Freeman, 1965b). The process is the same as that used to eliminate herd effects from daughter averages in sire evaluation and the methods used in New Zealand, Great Britain and New York State, have been recently reviewed by Searle (1964).

In brief, the principles of the deviation method used to adjust the present data are discussed below. The two models used are,

(1) (observed record - breed average) = (true record - breed average) + b(true herd level - breed average) + (error)

and,

(2) (true herd level) = (breed average) + B(observed herd average - breed average) + (error)

where,

b = the regression of observed records on their true herd levels,

B = the regression of true herd levels on the observed herd averages,

and observed records are 305 day, 2X, M. E. lactation records.

From (1), (true record) = (observed record) - $\hat{b}$ (true herd level -

breed average)

and substituting the estimate of (true herd level) from (2) for (true herd level) in the above,

(true record) = (observed record) - $\hat{b}$(breed average + $\hat{B}$(observed herd average - breed average) - breed average)

= (observed record) - $\hat{b}\hat{B}$(observed herd average - breed average), where $\hat{b}$ and $\hat{B}$ are the least squares estimates of b and B.

In the computations, the record of the cow concerned and those of her paternal half-sibs were excluded from the observed herd average or herd-mate average, to reduce the correlation between observed records and the estimated true herd levels. Since all available records of each cow were included in the herd-mate average, other close relatives, such as dams, could have had records starting in the same herd-year-season and therefore included in the average. These observed herd averages are herd-year-season averages and in the formulation they are deviated from their respective breed averages, each of which is one of the thirty-six Holstein year-season averages of all records available over the nineteen years from 1945 to 1963 inclusive. The optimum choice of two seasons of calving was determined by Bereskin (1963) as a seven month season from October to April inclusive and a five month season from May to September inclusive.

The estimated true herd level is the adjusted herd-mate average (AHA) of Bereskin (1963) and the regression coefficient, $\hat{B}$, is given

by $\frac{n}{n+a}$ where n is the number of records included in the herd-mate average and a is a constant ratio of variances. The adjustment is really for the size of the herd-mate group, the larger the group the better the estimate of true herd level. To adjust the data for the present study, a was put equal to 2 for milk and fat yield and equal to 3 for fat percentage.

Bereskin (1963) defines the regressed, adjusted, herd-mate average (RAHA) as follows;

RAHA = (breed average) + $\hat{b}$ (AHA - (breed average)) where $\hat{b}$ is the estimate of the regression of observed records on true herd levels as before and is taken as equal to 0.9, the value derived by Bereskin (1963), for all three production traits.

The true or adjusted record as a deviation from the appropriate breed average can now be found, the formula being,

(true record - breed average) = (observed record - breed average)
$- \hat{b}\hat{B}$(observed herd average - breed average)
= observed record - RAHA,

assuming that all breed-year-season averages are estimates of the same breed average. Thus the true record is expressed as a deviation of the observed record from the corresponding regressed, adjusted, herd-mate, or herd-year-season average.

The regressed, adjusted, herd-mate averages and the deviations for milk and fat yield were available as computed by W. R. Taylor. For fat percentage, the following procedure was adopted.

(a) The same seasons as those used for milk and fat yield were utilized. After a study of the lactation production averages for each month of calving as plotted by Bereskin and Freeman (1965a), it was decided that there would not be too much bias introduced if the same seasons were used, even although the curve for fat percentage was different from those for the yield traits. In an analysis of variance using the cross-classification of months and herds, Bereskin and Freeman (1965a) found only 1.1% of the variation in fat percentage associated with months, the comparative figures for milk and fat yields being 1.7% and 1.4% respectively. The optimum seasons for fat percentage would seem to be January to June and July to December inclusive (Bereskin and Hazel, ca. 1963). When the best seasonal breakdown for the yield traits (the one used in the present work) was used in a year-season cross-classification with herds in analysis of variance, only 0.2% of the variation in fat percentage was associated with year-season as compared with 2.3% for milk and 1.8% for fat yield. It seems that it might have been possible to raise the 0.2% to about 2% by adopting optimum seasons for fat percentage, but this did not seem worthwhile considering the small amount of variation associated with month or year-season of calving and the considerable extra computation involved.

(b) The deviations were calculated in two different ways.

These were,

(1) actual fat percentage - RAHA fat percentage

and

(2) actual fat percentage - $\frac{\text{RAHA fat yield}}{\text{RAHA milk yield}} \cdot 100$

Since the herd averages for milk and fat yield were not available as such and had to be calculated, determination of RAHA fat percentage was a lengthy process and it was thought that use of the second procedure might circumvent these calculations. If the RAHA is the best estimate of the fat or milk yield average for the herd-year-season, then the ratio of the two RAHAs as a percentage should be the best estimate of the fat percentage average for the herd-year-season. A consideration of the results from using the two procedures follows in section V.

V. REGRESSION OF OFFSPRING ON PARENT

A. Methods

First lactation records of 5,209 daughters and their dams were used to estimate the parent-offspring regressions. In cases of multiple offspring of one dam, the dam's record was repeated with each of the offspring. In the estimation of the regression of offspring on parent, this practice is valid if the correlation among the offspring of a parent is zero. But this correlation is a function of the square of the regression parameter and the correlation between deviations from regression of any two progeny of the same parent. This latter correlation is usually assumed zero under the normal analysis of variance assumption of uncorrelated errors, in which case the former correlation equals the square of the regression parameter. Kempthorne and Tandon (1953) have derived a weighted regression technique for the optimal (in terms of minimum sampling variance) estimation of the regression coefficient when each parent has an arbitrary number of offspring. The above authors, using data from the Iowa State University Holstein dairy herd, found little to choose between their method and the method of repeating the dam's record with each of the offspring, presumably because few cows had more than one daughter and because the estimated value of the correlation among the offspring of a parent was small. Bohren et al. (1961) confirmed this result with more extensive poultry data.

Heritability was estimated as twice the regression of offspring on dam. The expected composition of the estimate derived in this way is given by Dickerson (1959) for the random mating case and is an unbiased estimate of the proportion of additive genetic variance in the absence of locus by locus interactions (epistasis) and maternal effects contributing to the resemblance between daughters and dams. Of the 5,209 daughters, 576 had no sire identification. The remaining 4,633 daughters were the offspring of 1,011 sires, giving an average of 4.58 daughters per sire. The regressions were calculated utilizing all 5,209 pairs and also within sire of daughter groups using only the 4,633 pairs with sire identification for each daughter. Environmental correlations among individual cows due to herds, years, or seasons should have been removed by the use of deviations. That there remains a small bias in the parental variance is demonstrated below. Restricting the analysis to variation occurring within groups of dams mated to the same sire avoids biases due to departures from random mating (Lush, 1940). It was not determined in these data to what extent phenotypic assortive mating might have taken place. If there was any tendency for the better cows to be mated to the better bulls genetically, then the environmental correlations between daughters and dams due to daughters from better than average cows being given better than average care should be minimal within sire groups. Also, only in the case of full-sibs is it necessary to worry about errors introduced by repeating the dams' records with their daughters when the regressions are calculated within sire groups.

The random variables in the analyses are deviations of lactation records from regressed, adjusted herd-mate averages. Let the observed record of an animal be $Y_{ij} = \mathcal{M} + h_i + g_{ij} + e_{ij}$

where Y_{ij} is the record of the jth animal in the ith herd-year-season,

$\mathcal{M}$ is the breed average,

h_i is the effect peculiar to the ith herd-year-season,

g_{ij} is the breeding value of the jth individual in the ith herd-year-season,

and e_{ij} is random error associated with the jth record in the ith herd-year-season.

A new concept is introduced into the notation by letting the subscript (ij) represent the jth individual or record in the ith herd-year-season and treating the subscript as a single letter. The notation of the herd-mate averages is easier if a subscript r is introduced to represent an individual within the herd-mate group of the individual designated by the (ij) subscript. Thus the herd-mate average of the jth animal in the ith herd-year-season, or (ij)th animal, excluding the records of the animal and her paternal half-sibs, is represented as $HA_{(ij)}$.

$$HA_{(ij)} = \mathcal{M} + h_i + \frac{\sum_{r=1}^{n_{(ij)}} g_{(ij)r} + \sum_{r=1}^{n_{(ij)}} e_{(ij)r}}{n_{(ij)}}$$

where $g_{(ij)r}$ is the breeding value of the rth individual in the herd-mate group of the (ij)th animal,

$e_{(ij)r}$ is the corresponding random error,

and $n_{(ij)}$ is the number of herd-mates for the (ij)th animal.

The regressed, adjusted herd-mate average (RAHA) is

$$RAHA_{(ij)} = \mu + \frac{\hat{b} n_{(ij)}}{n_{(ij)} + a} \quad (HA_{(ij)} - \mu)$$

where $\hat{b}$ and a are as defined in section IV.

Let the deviation of the (ij)th record from the appropriate regressed, adjusted herd-mate average be $d_{(ij)}$.

Then, $d_{(ij)} = Y_{(ij)} - RAHA_{(ij)}$

$$= \mu + h_i + g_{(ij)} + e_{(ij)} - \left[\mu + \frac{\hat{b} n_{(ij)}}{n_{(ij)} + a} \left(\mu + h_i + \frac{\sum_{r=1}^{n_{(ij)}} g_{(ij)r} + \sum_{r=1}^{n_{(ij)}} e_{(ij)r}}{n_{(ij)}} - \mu \right) \right]$$

$$= \left(1 - \frac{\hat{b} n_{(ij)}}{n_{(ij)} + a} \right) h_i + g_{(ij)} - \frac{\hat{b}}{n_{(ij)} + a} \sum_{r=1}^{n_{(ij)}} g_{(ij)r}$$

$$+ e_{(ij)} - \frac{\hat{b}}{n_{(ij)} + a} \sum_{r=1}^{n_{(ij)}} e_{(ij)r}$$

For the derivation of the variance among dam records, $d_{(ij)}$ is the deviation of the (ij)th dam from her regressed, adjusted herd-mate average, and (ij) equals 1, 2, ..., N when there are N dams. In the

subsequent formulations, E stands for "expectation of".

$$E\left[\text{calculated variance } (d_{(ij)})\right] = \frac{1}{N-1} E\left[\sum_{(ij)} d_{(ij)}^2 - \frac{1}{N} E\left(\sum_{(ij)} d_{(ij)}\right)^2\right]$$

$$= \frac{1}{N-1}\left[E \sum_{(ij)} d_{(ij)}^2 - \frac{1}{N}\left(E \sum_{(ij)} d_{(ij)}^2 + E \sum_{(ij)} \sum_{(ij)'} d_{(ij)}\, d_{(ij)'}\right)\right], \quad (ij) \neq (ij)'.$$

In the following expectations, the presence of an r in the subscript indicates that herd-mates are being considered.

Let $E(h_i)^2 = \sigma_h^2$,

$E(g_{(ij)})^2 = E(g_{(ij)r})^2 = \sigma_g^2$,

$E(e_{(ij)})^2 = E(e_{(ij)\,r})^2 = \sigma_e^2$,

$E(h_i) = E(g_{(ij)}) = E(g_{(ij)r}) = E(e_{(ij)}) = E(e_{(ij)r}) = 0$,

$E(g_{(ij)})(g_{(ij)r})$ = the expectation of the product of the breeding value of a dam and the breeding value of one of her herd-mates = σ_{gg_r},

$E(g_{(ij)r})(g_{(ij)r'})$ = the expectation of the product of the breeding values of one of the herd-mates of a dam and another of the herd-mates of the same dam $= \sigma_{g_r g_{r'}}$,

and all other expectations of products be zero.

Considering only the first term in the square brackets in the expectation of the calculated variance above,

$$E \sum_{(ij)} d_{(ij)}^2 = \sum_{(ij)} \Bigg[\left(1 - \frac{\hat{b} n_{(ij)}}{n_{(ij)} + a}\right)^2 \sigma_h^2 + \sigma_g^2 + \frac{n_{(ij)}^2 \hat{b}^2}{(n_{(ij)} + a)^2} \sigma_g^2 - \frac{2n_{(ij)} \hat{b}}{n_{(ij)} + a} \sigma_{gg_r} + \frac{n_{(ij)} (n_{(ij)} - 1) \hat{b}^2}{(n_{(ij)} + a)^2} \sigma_{g_r g_{r'}} + \sigma_e^2 + \frac{n_{(ij)}^2 \hat{b}^2}{(n_{(ij)} + a)^2} \sigma_e^2 \Bigg]$$

σ_{gg_r} is the genotypic covariance between a dam and her herd-mates while $\sigma_{g_r g_{r'}}$ is the genotypic covariance among herd-mates.

The expectation of the calculated variance of $d_{(ij)}$ can now be written

$$E\left[\text{calculated } V(d_{(ij)})\right] = \sum_{(ij)} \frac{1}{N} \Bigg[\left(1 - \frac{\hat{b} n_{(ij)}}{n_{(ij)} + a}\right)^2 \sigma_h^2 + \left(1 + \frac{n_{(ij)}^2 \hat{b}^2}{(n_{(ij)} + a)^2}\right) (\sigma_g^2 + \sigma_e^2) - \frac{2n_{(ij)} \hat{b}}{n_{(ij)} + a} \sigma_{gg_r} + \frac{n_{(ij)} (n_{(ij)} - 1) \hat{b}^2}{(n_{(ij)} + a)^2} \sigma_{g_r g_{r'}} \Bigg] - \frac{1}{N(N-1)} E\left(\sum_{(ij)} \sum_{(ij)'} d_{(ij)} d_{(ij)'} \right).$$

Freeman (1964) has described the last term in the above equation as made up of covariances among the deviation records of the different dams and he concludes that it can be considered zero without adding undue bias to the result.

For the derivation of the covariance between daughters and dams, $d_{(ij)}$ is the deviation of the (ij)th dam and $d'_{(ij)}$ the corresponding daughter deviation. The presence of the same subscript on daughters and dams merely indicates the relationship and is not intended to imply that daughters and dams are in the same herd-year-season, since this is impossible.

$$E\left[\text{calculated covariance } (d_{(ij)}, d'_{(ij)})\right] = \frac{1}{N-1}\left[E\sum_{(ij)} d_{(ij)}d'_{(ij)} - \frac{1}{N}E\left(\sum_{(ij)} d_{(ij)}\sum_{(ij)} d'_{(ij)}\right)\right]$$

$$= \frac{1}{N-1}\left[E\sum_{(ij)} d_{(ij)}\,d'_{(ij)} - \frac{1}{N}\left(E\sum_{(ij)} d_{(ij)}\,d'_{(ij)} + E\sum_{(ij)}\sum_{(ij)'} d_{(ij)}\,d'_{(ij)'}\right)\right], \quad (ij) \neq (ij)'.$$

In the following expectations, a prime on a g indicates a daughter, no prime indicates a dam, and the subscript r again indicates that herd-mates are being considered.

Let $E(g_{(ij)})(g'_{(ij)}) = \sigma_{gg'}$

$E(g_{(ij)})(g'_{(ij)r}) = \sigma_{gg'_r}$

$E(g'_{(ij)})(g_{(ij)r}) = \sigma_{g'g_r}$

$$E(g_{(ij)r})(g'_{(ij)r}) = \sigma g_r g'_r$$

and all other expectations of products be zero. Again considering only the first term in the square brackets in the expectation of the calculated covariance above,

$$E \sum_{(ij)} d_{(ij)} d'_{(ij)} = \sum_{(ij)} \left(\sigma gg' - \frac{n'_{(ij)} \hat{b}}{n'_{(ij)} + a} \sigma gg'_r - \frac{n_{(ij)} \hat{b}}{n_{(ij)} + a} \sigma g'g_r + \frac{n_{(ij)} n'_{(ij)} \hat{b}^2}{(n_{(ij)} + a)(n'_{(ij)} + a)} \sigma g_r g'_r \right).$$

The four covariance terms in the above right hand side are, respectively, (1) the genotypic covariance between a dam and her daughter, (2) the genotypic covariance between a dam and the herd-mates of her daughter, (3) the genotypic covariance between a daughter and the herd-mates of her dam, and (4) the genotypic covariance between the herd-mates of a daughter and the herd-mates of her dam.

The expectation of the calculated covariance can now be written,

$$E\left[\text{calculated } \mathrm{Cov}(d_{(ij)}, d'_{(ij)})\right] = \sum_{(ij)} \frac{1}{N} \left(\sigma gg' - \frac{n'_{(ij)} \hat{b}}{n'_{(ij)} + a} \sigma gg'_r - \frac{n_{(ij)} \hat{b}}{n_{(ij)} + a} \sigma g'g_r + \frac{n_{(ij)} n'_{(ij)} \hat{b}^2}{(n_{(ij)} + a)(n'_{(ij)} + a)} \sigma g_r g'_r \right) - \frac{1}{N(N-1)}$$

$$E\left(\sum_{(ij)} \sum_{(ij)'} d_{(ij)} d'_{(ij)'} \right).$$

Again, the last term in the above right hand side of the calculated covariance can be considered zero as was done for the corresponding term in the calculated variance, following the conclusion of Freeman (1964).

For simplification in the evaluation of the regression of daughter on dam, let all $n_{(ij)} = n_{(ij)'} = n'_{(ij)} = n'_{(ij)'} = n$.

Now, the expectation of the calculated regression coefficient is

$$E(\hat{B}) = \frac{\sigma_{gg'} - \frac{n\hat{b}}{n+a}(\sigma_{gg'_r} + \sigma_{g'g_r}) + \frac{n^2\hat{b}^2}{(n+a)^2}\sigma_{g_rg'_r}}{(1 - \frac{\hat{b}n}{n+a})^2\sigma_h^2 + (1 + \frac{n\hat{b}^2}{(n+a)^2})(\sigma_g^2 + \sigma_e^2) - 2\frac{n\hat{b}}{n+a}\sigma_{gg_r} + \frac{n(n-1)\hat{b}^2}{(n+a)^2}\sigma_{g_rg_{r'}}}$$

It remains to evaluate the various variance and covariance terms, and their coefficients, in the above expectation.

The average value for the size of the herd-mate group of the daughters and dams used in this study was approximately twenty. Taking $n = 20$, $\hat{b} = 0.9$ and $a = 2$, the expectation of the regression coefficient becomes

$$E(\hat{B}) = \frac{\sigma_{gg'} - 0.82(\sigma_{gg'_r} + \sigma_{g'g_r}) + 0.67\sigma_{g_rg'_r}}{0.03\sigma_h^2 + 1.03(\sigma_g^2 + \sigma_e^2) - 1.64\sigma_{gg_r} + 0.64\sigma_{g_rg_{r'}}}$$

As n becomes larger, the coefficient of σ_h^2 in the denominator approaches zero while the coefficient of $(\sigma_g^2 + \sigma_e^2)$ approaches unity.

The genotypic covariance between the herd-mates of a daughter and the herd-mates of her dam ($\sigma_{g_rg'_r}$) is not likely to be large,

but there could be some animals in common to the two groups, represented by different lactations since the daughter and dam are both in the same herd (not herd-year-season), or there could be related animals in the two groups. The genotypic covariances between a dam and the herd-mates of her daughter ($\sigma gg'_r$) and between a daughter and the herd-mates of her dam ($\sigma g'g_r$) are also not likely to be large on the average and will probably be smaller than $\sigma g_r g'_r$. The former two covariances probably more than cancel the effects of $\sigma g_r g'_r$, since the coefficients are of opposite sign. Since the covariances are likely to be very small, their coefficients are less than unity, and they partly cancel each other, their effect in the numerator is unlikely to be more than a tiny negative amount.

The genotypic covariance among herd-mates ($\sigma g_r g_{r'}$) is likely to be the largest of the covariance terms. There is no easy way of evaluating this term but a herd-mate group will almost certainly include some pairs of half-sibs and other assorted pairs of relatives. In a study of the use of deviation records in half-sib analyses, Van Vleck et al. (1961) assumed that every individual within a herd-mate group had a different sire, and stated that although the assumption does not strictly hold in practice, the error involved in making it is small. Freeman (1964) has looked at the covariance in terms of the additive genetic variance and concludes from a study of the literature that the coefficient of the variance is probably less than 0.10, making the effect of the covariance small.

The remaining covariance term in the denominator has a coefficient of opposite sign and twice the magnitude of that of $\sigma_{g_r g_{r'}}$. This is the genotypic covariance between a dam and her herd-mates (σ_{gg_r}), and the size of this covariance has been minimized by the removal of the record of the dam and her half-sibs from the herd-mate group. However, as mentioned in section IV, other close relatives of the dam could have records starting in the same herd-year-season. Although no precise estimates are available as to the relative sizes of these covariance terms, it is believed that the two terms in the denominator largely cancel the effects of each other.

Taking the above discussion into account and eliminating the covariance terms discussed, the expectation of the regression coefficient becomes

$$E(\hat{B}) = \frac{\sigma_{gg'}}{0.03\,\sigma_h^2 + 1.03(\sigma_g^2 + \sigma_e^2)}$$

and, since the genotypic covariance between daughter and dam is approximately equal to half of the additive genetic variance, the expectation approximates

$$1/2 \quad \frac{\sigma_g^2}{\sigma_g^2 + \sigma_e^2}$$

which is one half of the heritability.

In order to illustrate the magnitude of the bias present in

the formula

$$\sigma^2_h = \frac{\sigma^2_g}{0.03\sigma^2_h + 1.03(\sigma^2_g + \sigma^2_e)}$$

the following approximate values taken from Bereskin and Freeman (1965a) were used to calculate heritabilities in this particular case with n = 20, $\hat{b}$ = 0.9 and a = 2.

	milk yield deviation	fat yield deviation	fat percentage deviation
σ^2_h	23,000	3,200	0.02
σ^2_g	11,000	1,200	0.05
σ^2_e	44,000	5,700	0.09

Heritabilities were calculated using the biased formula and the unbiased formula $\left(\frac{\sigma^2_g}{\sigma^2_g + \sigma^2_e}\right)$, and compared as follows:

	unbiased	biased	difference
Milk yield	0.200	0.192	0.008
Fat yield	0.174	0.167	0.007
Fat percentage	0.357	0.345	0.012

It can readily be seen that with n as large as twenty, the biases are very small.

The model for the within-sire regression analysis was

$$d'_{i(jk)} = M_i + S_i + B(d_{i(jk)} - \bar{d}_i) + e_{i(jk)}$$

where $d'_{i(jk)}$ is the deviation record of the (jk)th daughter of the ith sire, the (jk)th daughter being the kth

animal in the jth herd-year-season,

M_i is the mean of the daughters of the ith sire,

S_i is the effect peculiar to the ith sire,

B is the regression coefficient,

$d_{i(jk)}$ is the deviation record of the (jk)th dam in the ith sire's group,

$\bar{d}_i$ is the mean of the dams mated to the ith sire,

and $e_{i(jk)}$ is random error associated with the (jk)th daughter record in the ith sire's group,

$(jk) = 1, 2, \ldots, n_i$; $i = 1, 2, \ldots, s$.

The sums of products, sums of squares, and corrections for the mean and sire effect were computed within each sire's group, and pooled over groups. This procedure gives an unbiased estimate of B assuming $B_i = B_{i'}$ for all i, i'. Within each group, the variances of $d'_{i(jk)}$ and $d_{i(jk)}$ have $n_i - 1$ degrees of freedom and there are $n_i - 2$ degrees of freedom associated with error. Pooled over the s groups, this gives $\sum_i n_i - s$ and $\sum_i n_i - 2s$ degrees of freedom respectively.

B. Results and Discussion

Results from the regression analysis using all 5,209 pairs are given in Tables 1 and 2. Fat percentage 1 refers to the deviation of actual fat percentage from the regressed, adjusted herd-mate average for fat percentage. Fat percentage 2 refers to the deviation of actual fat percentage from the percentage that the RAHA fat yield is of the RAHA milk yield, as described in section IV. Fat and milk refer to the deviations from the appropriate herd-mate averages. Results from the within-sire regression analysis are similarly given in Tables 3 and 4.

Table 1. Parent and offspring mean deviations and standard deviations of observations for milk, fat and fat percentage from 5,209 pairs

	Parent		Offspring	
	Mean	Standard Deviation	Mean	Standard Deviation
Milk (lbs)	638.7	2390.3	106.1	2399.6
Fat (lbs)	28.6	85.3	8.9	86.6
Fat percentage 1	0.06	0.31	0.06	0.32
Fat percentage 2	0.06	0.31	0.05	0.32

Table 2. Regression coefficients and standard errors from regression of daughter on dam

Offspring Trait	Parental Trait: milk		fat		fat percentage 1		fat percentage 2	
milk	0.1935	± 0.01365	0.4208	± 0.03857	-73.5798	± 10.6637	-73.2996	± 10.6231
fat	0.0586	± 0.00495	0.1842	± 0.01384	9.6889	± 3.8601*	9.5977*	± 3.8545
fat percentage 1	-0.0001	± 0.00002	0.0002	± 0.00004	0.2901	± 0.0135	0.2882	± 0.0135
fat percentage 2	-0.0001	± 0.00002	0.0002	± 0.00005	0.2864	± 0.0136	0.2850	± 0.0135

*Coefficient significantly greater than zero ($P < 0.05$) by "t" test (5,207 df). All other coefficients highly significant ($P < 0.01$).

It should be noted that when the pairs with no sire identification on the daughters are included in the data, the mean deviations for parent and offspring milk and fat (Table 1) are lower than when these pairs are excluded (Table 3), but the variances are greater for all traits. It is perhaps not unexpected that animals from herds with less information would have lower yields and that inclusion of these lower yielding animals would increase the phenotypic variance.

Table 3. Parent and offspring mean deviations and standard deviations of observations for milk, fat and fat percentage from the 4,633 pairs with sire identification on the daughters

	Parent		Offspring	
	Mean	Standard Deviation	Mean	Standard Deviation
Milk (lbs)	662.2	2306.2	157.3	2265.2
Fat (lbs)	29.6	82.0	10.8	81.9
Fat percentage 1	0.06	0.30	0.06	0.29
Fat percentage 2	0.06	0.30	0.05	0.29

Table 4. Regression coefficients and standard errors from within-sire regression of daughter on dam

Offspring Trait	Parental Trait: milk	fat	fat percentage 1	fat percentage 2
milk	0.1766 ± 0.01891	0.4039 ± 0.05342	-54.2709 ± 14.7075	-53.2768 ± 14.6364
fat	0.0501 ± 0.00687	0.1725 ± 0.01925	16.6756 ± 5.3276	16.8804 ± 5.3083
fat percentage 1	-0.0001 ± 0.00002	0.0002 ± 0.00007	0.2815 ± 0.0177	0.2799 ± 0.0177
fat percentage 2	-0.0001 ± 0.00002	0.0002 ± 0.00007	0.2790 ± 0.0178	0.2778 ± 0.0177

All of the above coefficients significantly greater than zero ($P < 0.01$) by "t" test (2,611 df).

Since all of the records are deviations from averages, the means are expected to be close to zero. In fact, they are all positive by up to one third of a standard deviation, with the parental means being greater than the offspring means for the yield traits. If the paternal half-sibs of an above average cow are above average and the herd-mate number is small, removal of the records of the cow and her sibs from the herd-year-season data will lower this average and give the cow a higher positive deviation. If the opposite is true for a below average cow and she happens to be a cow with sire unknown, the records of her (unknown) half-sibs will remain in the herd-year-season average and her negative deviation will be reduced. Such effects could contribute to positive means. The daughter-dam pairs are selected from among the records used to determine the herd-year-season averages, and this selection could have been in such a way as to result in a greater proportion of above average animals being included in the paired data than below average animals. This likewise could contribute to positive means. Finally, the paired data are first lactation records deviated from averages made up of records from all lactations and, if first records are higher than later records on a mature equivalent basis because of selection or inaccurate age correction, then positive means might be expected.

The higher dam records are most probably due to selection of the dams, the poorer dams not having daughters with first lactation records. Regression towards the mean would then automatically

give lower values for the daughters. Bradford and Van Vleck (1964) found positive mean values for dams and negative values for daughters and have discussed this latter point in more detail. The variances of daughter and dam deviations are not far from equal in all traits, suggesting that the variance of genetic values for the sires is similar to that of the dams.

The heritabilities found by doubling the regression coefficients are given in Table 5. The standard errors were found by doubling the usual standard errors of the regression coefficients.

The heritabilities estimated from the total data are higher for all traits than those estimated within-sires. This could suggest that some phenotypic assortive mating had taken place. The within-sire heritabilities are given more favorable consideration and within-sire analyses are used subsequently, simply because, in theory, they should be more accurate estimates. They are slightly more conservative. In a survey of the literature from various countries utilizing data from various breeds, Johansson (1961) reports values of heritability for milk and fat yield calculated from daughter-dam regression within herds and sires of from 0.20 to 0.43. Values for fat percentage range from 0.43 to 0.76. In most studies of the separate lactations, the heritabilities of first lactation records are higher than those for subsequent lactations (Johansson, 1961; Molineuvo and Lush, 1964). With Holstein cattle in the United States, Freeman (1960) working with 1,876 pairs found heritabilities

of first lactation records to be 0.36, 0.43 and 0.63 for milk, fat and fat percentage respectively; Clark and Touchberry (1962) with 385 pairs found values of 0.44 and 0.40 for milk and fat; while Tabler and Touchberry (1959) with 20,024 pairs found values of 0.27, 0.24 and 0.57 for milk, fat and fat percentage. The values found in this study are therefore not inconsistent with those obtained by previous workers. However, Bereskin and Freeman (1965a), using data from the same sources as the present author, found heritabilities estimated from regressions of daughter's average record on dam's average record within herd-year-seasons for milk yield, fat yield and fat percentage to be 0.220 ± 0.040, 0.180 ± 0.042 and 0.526 ± 0.036 respectively. These estimates from 4,178 pairs are considerably lower than the estimates from the present study. If it is true that estimates from first lactation records are higher than those from later records, it might be expected that estimates based on life-time averages should also be lower. Use of the formula of Lush and Straus (1942) to adjust the estimates to a single-record basis further lowers the values of the estimates.

Genetic correlations among milk deviation, fat deviation and the second measure of fat percentage deviation were calculated from the formula of Hazel (1943) as the geometric averages of

the two possible genetic correlations between each pair of traits, and using the within-sire regression coefficents. Standard errors can be attached to such correlation coefficients derived from daughter-dam regression by means of equation (13) of Reeve (1955). This equation (formula 1) can be simplified by assuming that the genetic correlation (r_G) is approximately equal to the phenotypic correlation (r_p) and that $h_1 h_2$ is approximately equal to $\frac{2\, h_1^2\, h_2^2}{h_1^2 + h_2^2}$, where h_1^2 and h_2^2 are the heritabilities of the two traits concerned. The simplified equation (formula 2) was derived by the present author. With further approximation and simplification, the formula of Falconer (1960) can be derived (formula 3). The results from an empirical sampling study by Van Vleck and Henderson (1961) indicate that formula 1 is accurate when the size of sample is 1,000 or more. Formula 3 was derived by Robertson (1959).

Since phenotypic correlations were not obtained from the regression analysis, it was decided to compare the three formulae to see whether or not either formula 2 or formula 3 could be used in this study. For comparative purposes, the most extreme differences between the heritabilities and between the genetic and phenotypic correlations likely to be encountered in the course of study were utilized. The traits chosen were fat yield and fat percentage with heritabilities 0.34 ± 0.038 and 0.57 ± 0.035, and with r_G equal to 0.26 and r_p equal to 0.16. The relation between the chosen values of r_G and r_p is consistent with the

corresponding relation found reported in the relevant literature (Blanchard, 1965; Tabler and Touchberry, 1959; Wilcox et al.,1962). The three values obtained for the sampling errors were 0.0499 using formula 1, 0.0483 using formula 2, and 0.0546 using formula 3. Because of these results and the overall small sizes of the sampling errors (due largely to the large sample size), it was decided to use the approximate formula 2 in subsequent work. This formula 2 is given as:

$$\text{Variance}(r_G) = \frac{(1-r_G^2)^2}{N-S}\left(\frac{1}{2} + \frac{2}{C^2} - \frac{1}{2C}\right)$$

where N is the total number of daughter-dam pairs,

S is the number of sires of daughters,

and C is equal to $\sqrt{h_1^2 h_2^2}$.

The genetic correlations and their standard errors are given in Table 5.

Like the heritability estimates, the values obtained for the genetic correlations are not inconsistent with those obtained by previous workers. Again citing studies using Holstein data in the United States, Farthing and Legates (1957), using 5,458 daughter-dam pairs, found a value of -0.38 ± 0.06 for the genetic correlation between milk yield and fat percentage; Tabler and Touchberry (1959) found values of 0.77 ± 0.018 between milk and fat, -0.33 ± 0.025 between milk and fat percentage, and 0.34 ± 0.025 between fat yield and fat percentage; Clark and Touchberry (1962)

found the genetic correlation between milk and fat yield to be 0.86 ± 0.08. As an example of results from half-sib analysis, Blanchard (1965) with deviation lactation records from 8,271 daughters of 770 bulls found genetic correlations of 0.74 between milk and fat yield, -0.38 between milk and fat percentage, and 0.34 between fat yield and fat percentage.

Table 5. Estimates of heritability and genetic correlations among milk, fat and fat percentage deviations from daughter-dam regression analysis

	Heritability Estimates	
Trait	All Data	Within-sires Analysis
Milk	0.387 ± 0.027	0.353 ± 0.038
Fat	0.368 ± 0.028	0.345 ± 0.038
Fat percentage 1	0.580 ± 0.027	0.563 ± 0.035
Fat percentage 2	0.570 ± 0.027	0.556 ± 0.035
Genetic Correlations	(within-sires analysis)	
Milk X Fat	0.815 ± 0.0219	
Milk X Fat Percentage 2	-0.330 ± 0.0458	
Fat X Fat Percentage 2	0.265 ± 0.0483	

In whichever ways the two measures of fat percentage used in the above analysis are compared, there is little to pick and choose between them. This is so whether they are compared by variances or by means, by regressions or by the standard errors of regressions. The within-sire genetic correlation between the two traits was computed as 0.9993 ± 0.00008. On the basis of this evidence it was decided to use only the simpler of the two measures, the deviation of actual fat percentage from the percentage that the RAHA fat yield is of the RAHA milk yield for the particular herd-year-season, in subsequent analyses.

The within-sire regression coefficients, heritability estimates, genetic correlations, means and variances found from the previous analyses are used as reference bases for the subsequent analyses in this study.

VI. GROUPING OF THE DATA

In order to study the frequency distributions of the traits and to facilitate the making of certain types of transformation of scale (in particular those to maximize the heritabilities), the data were grouped, giving to the variables a discontinuous form.

Two-way classifications were made with the daughter deviation record as one classification and the dam deviation record as the other classification. This was done for each of the three traits. The model used within each classification was simply

$$Y_i = \mu + e_i$$

where Y_i is the value for the midpoint of the group in which the record of the animal falls,

μ is the value for the mean of the population of midpoint values, and

e_i is a random error associated with the ith midpoint value and has expectation zero and variance σ^2, so that σ^2 is the variance of the population of midpoint values,

$i = 1, 2, \ldots, N$ where N represents the number of groups in each classification.

After some trial and error, it was decided to make thirty groups each way with ranges and group widths for each classification of the three traits as follows:

Milk yield from -8250 lbs. to +8250 lbs. by 550 lbs,

Fat yield from -330 lbs. to +330 lbs. by 22 lbs,

Fat percentage from -1.0% to +1.7% by 0.09%.

All 5,209 pairs were used in this grouping but a few records were beyond the ends of the range.

For the purposes of studying the distributions of the data (of the e_i of the model), the daughter frequency totals were used because some of the dam records were repeated with more than one daughter. The analysis of these distributions is an example of analysis of residuals as discussed by Anscombe and Tukey (1963).

The distributions based on 5,200; 5,204; and 5,209 deviation records for milk, fat and fat percentage are given in Figures 1, 2, and 3 in terms of the percentages of records falling in each group. Large random samples from single populations will reflect quite accurately the shapes of the population distributions and enable the population parameters to be estimated (Snedecor, 1956). It is the assumption here that the sample of daughter records is a large random sample from the population of Mid-Western Holstein first lactation records.

Procedures for computing the mean and variance of each distribution and tests for departures of the distributions from normal are given in Snedecor (1956). Tests were made for skewness and for kurtosis. The statistics involved are g_1 and g_2, to which standard errors can be attached in order to test the diff-

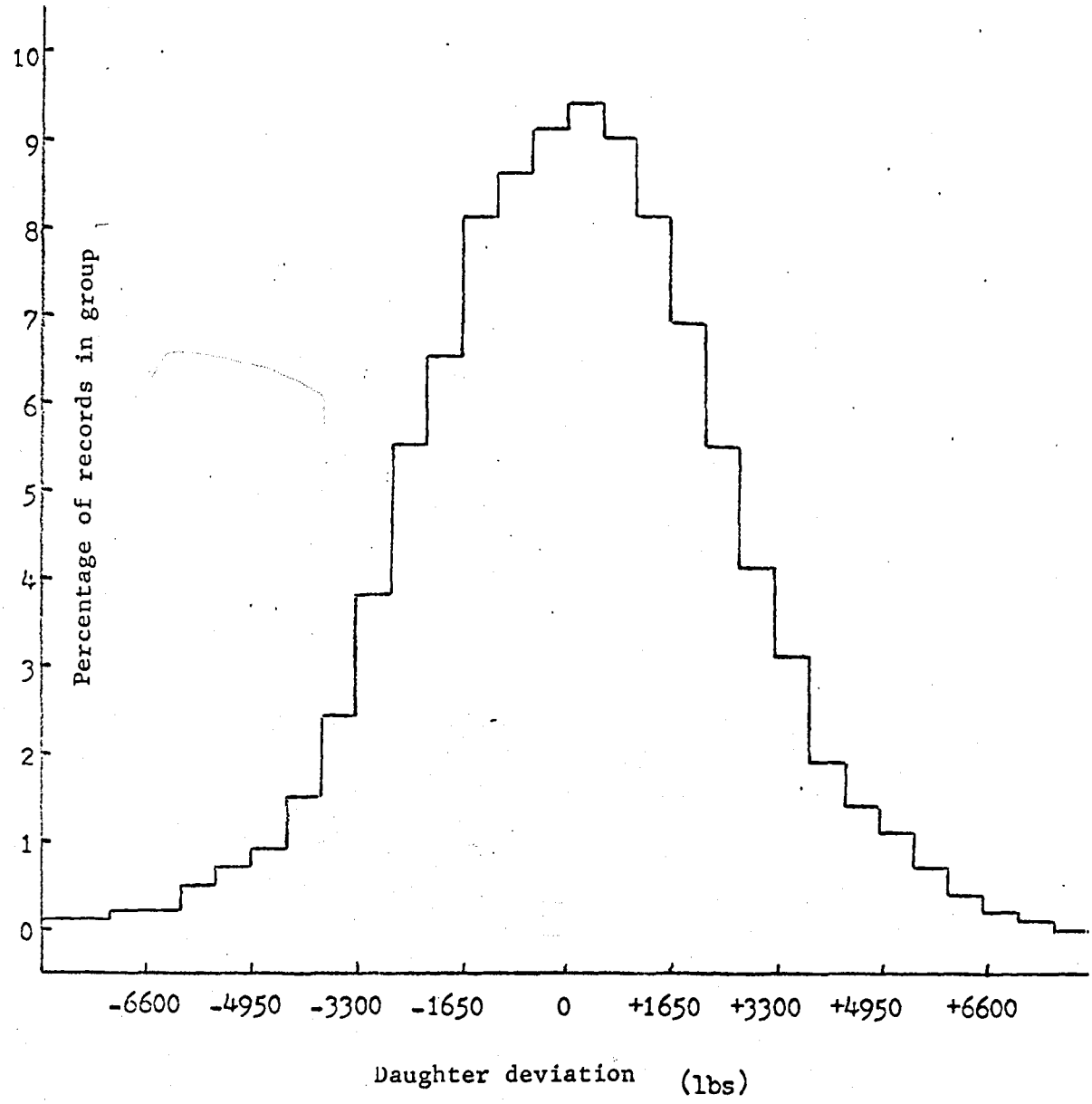

Figure 1. Frequency distribution of daughter milk yield deviation records

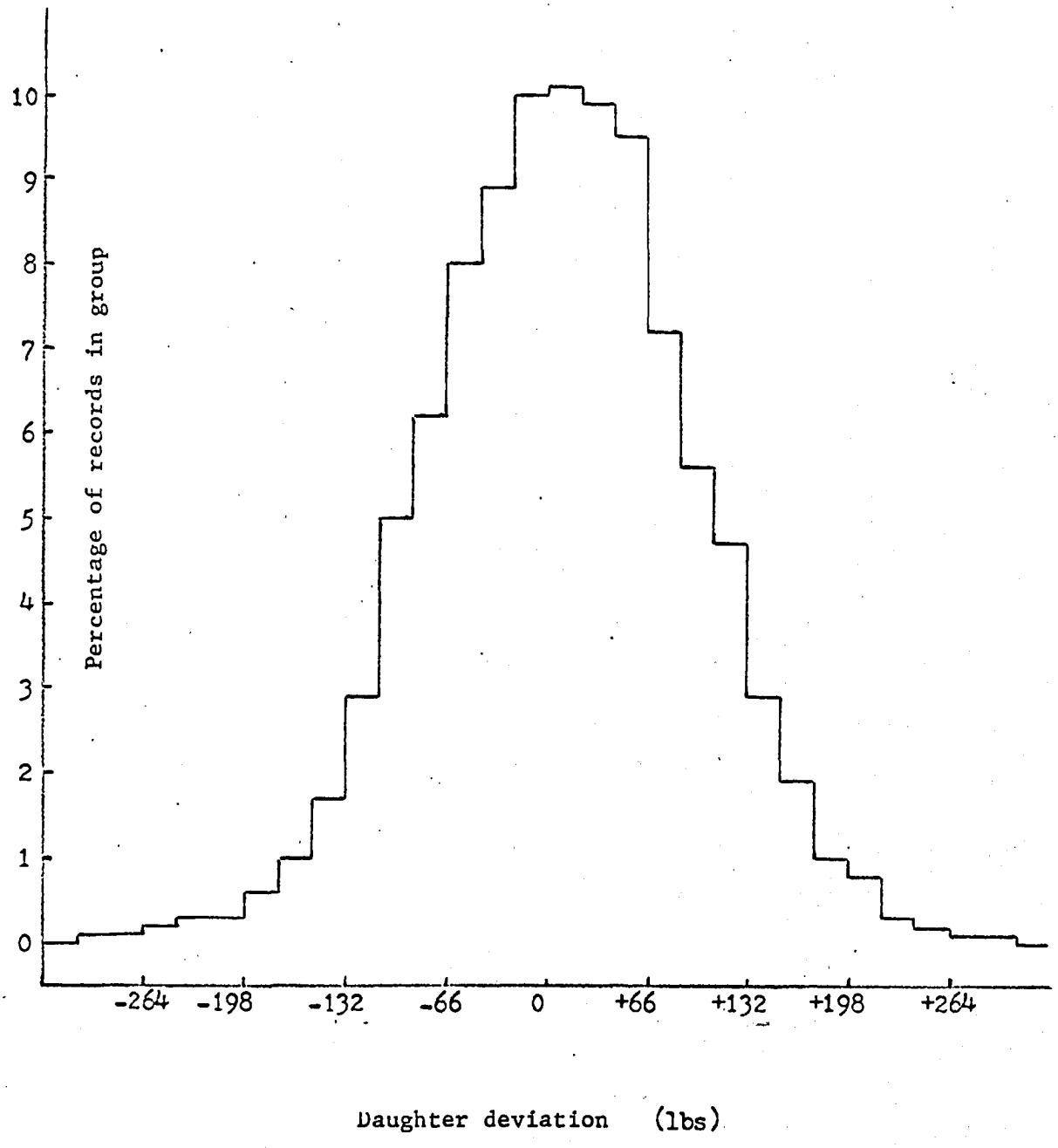

Figure 2. Frequency distribution of daughter fat yield deviation records

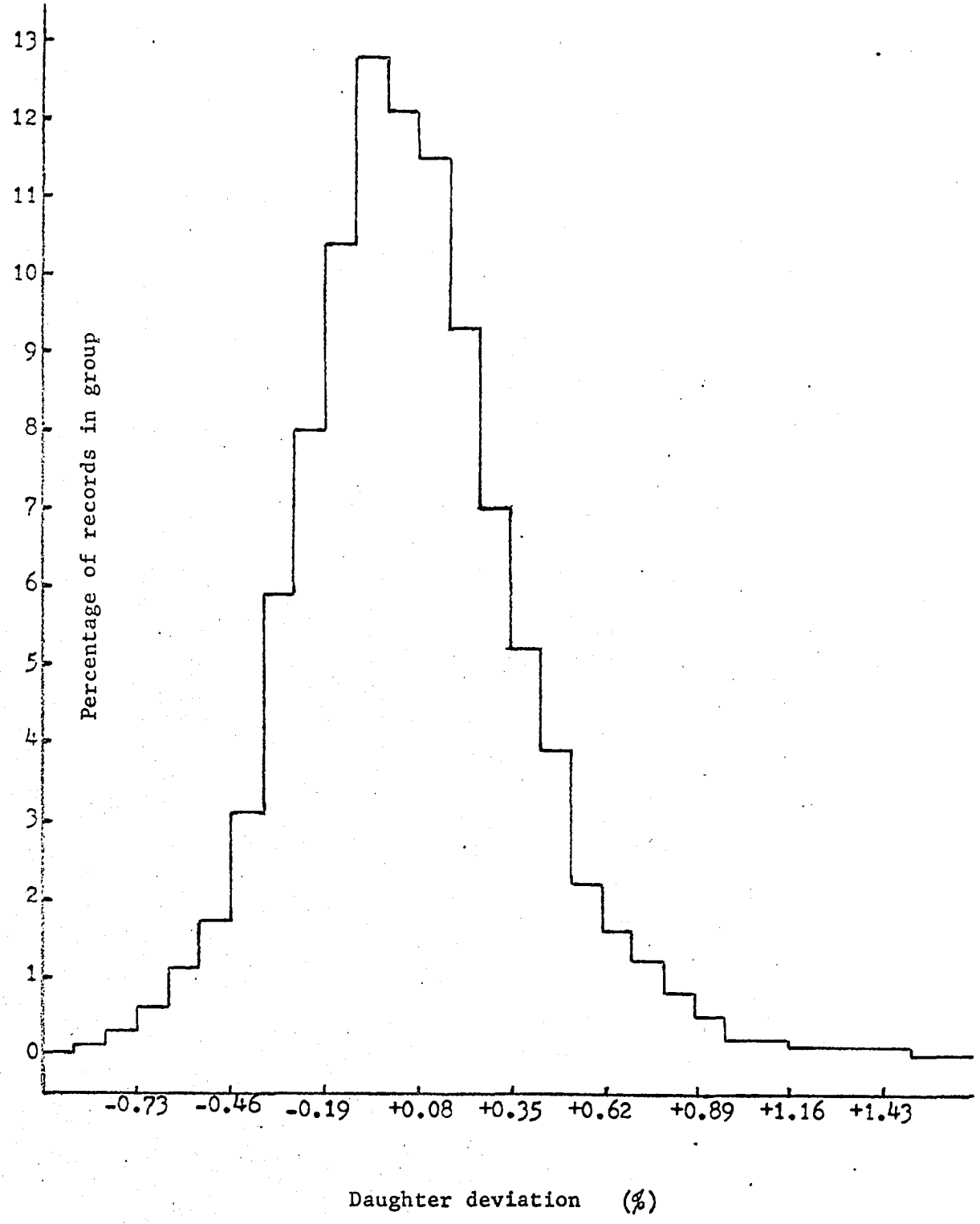

Figure 3. Frequency distribution of daughter fat percentage deviation records

erences of the estimates from zero by means of Student's "t".

For milk yield deviation, with 30 groups given coded values from -15 to +14 in units of one, the mean was -0.28 and the standard deviation 4.32 units. In terms of the original units, these estimates are 118.4 lbs. and standard deviation 2376.4 lbs. These compare with the values given in Tables 1 and 3.

Snedecor (1956) suggests that grouping of the data gives sufficient precision of estimation of parameters if the sample standard deviation is at least four times as great as the group interval. It can be seen that this criterion is fulfilled in the present case, the group interval being 550 lbs.

In terms of the coded units $\hat{g}_1$ was 0.00827 with variance 0.00115 and $\hat{g}_2$ 0.17047 with variance 0.00461. The former was not significant but the latter was significant at the 5% level by "t" test with infinite degrees of freedom. This positive g_2 suggests a slight excess of items near the mean and far from it, with a corresponding depletion of the flanks of the distribution. In other words the distribution is slightly peaked. There is no evidence for skewness.

For fat yield deviation, with 30 groups coded in the same way as for milk yield, the mean was -0.06 and the standard deviation was 3.915 units. Again in terms of the original units, these estimates are 9.64 lbs. and standard deviation 86.14 lbs. These compare well with the estimates in Tables 1 and 3 and the standard

deviation is approximately four times the group interval of 22 lbs.

The values found for $\hat{g}_1$ and $\hat{g}_2$ were -0.04933 and 0.25094 with variances 0.00115 and 0.00461. The former was not significant but the latter was, this time at the 1% level. The distribution therefore departed from normality in a peaked fashion and again there was no evidence for skewness.

For fat percentage deviation, the two largest groups were combined into one (for convenience in later transformations) giving 29 groups which were coded in units of one from -11 to +17.

The mean in coded units was 0.22 and the standard deviation 3.52 units. In terms of the original percentage units, these estimates are 0.055% and 0.317%, comparing favorably with the estimates in Tables 1 and 3. Here the standard deviation is only 3.5 times the group interval of 0.09% so that the grouping falls somewhat short of maximum desirability by Snedecor's criterion.

The estimates of g_1 and g_2 were 0.46357 and 0.92101 with variances 0.00115 and 0.00460 respectively. Both values were highly significant by "t" test. The interpretation is that the distribution is peaked and is asymmetric with an excess of items smaller than the mean, drawing the peak of the frequency curve to the left.

In summary, the distributions of milk and fat yield deviations are symmetric but slightly peaked as compared to the normal curve. Fat percentage deviations are peaked and also skewed with

the tail to the high values of the distribution. Bradford and Van Vleck (1964) show a frequency distribution of milk yield deviations from season-herdmate averages of 5,740 cows which has no evidence of skewness and is similar to the distribution in Figure 1. Ramsay (1964) found the distribution of unselected Iowa Holstein first lactation milk yields to be very slightly skewed with a tail of lower milk yields. However, the departures, if any, from symmetry in the above two studies, as in the present study, are very small. On the other hand, Gowen (1924) showed the distributions of records of Holstein Advanced Registry cows to be markedly skewed for milk yield and slightly skewed for butterfat percentage. However, these records were not representative since, to enter the Advanced Registry, cows had to produce above a minimum standard. Both distributions had tails of high values, and this would appear to be the most likely form of asymmetry to be encountered, if asymmetry is present at all, because of the effects of selection.

As mentioned before, one of the major assumptions in linear regression analysis is that the variances among the Y values (dependent variate) are the same for each fixed X value (independent variate). This is the assumption of equal or homogeneous variances discussed by Eisenhart (1947). As Snedecor (1956) puts it, for each X there is a population of Y's, and all these sampled populations have a common variance. In discussing the possibility

of heterogeneity of error variances, Cochran (1947) mentions a common type of heterogeneity arising from non-normality in the distribution of errors and in which the variance of an observation is some simple function of it's mean value. The present grouped data were utilised to investigate the assumption of homogeneous variance and the possible relation between variance and mean.

For each of the three traits, the dam groups were consolidated into twelve in order to have as equal numbers as possible among the groups. The ranges of numbers in the groups were 338-499 for milk, 243-571 for fat and 237-624 for fat percentage. The daughter variance based on the original breakdown into thirty groups was then calculated for each dam group. These variances are listed in Table 6 in ascending order of dam group mean and are in coded units. With correlation between daughter and dam records, it is expected that daughter variances should be higher in the dam groups with the wider group intervals. However, the consolidation of the dam groups was done in such a way that group intervals remained equal except for the top two of the twelve for all three traits, the bottom two for milk and fat, and the bottom one for fat percentage. A close examination of the three bivariate distributions led to the conclusion that, since the correlations are very low (especially in the extremities of the distributions), any differences in variance due to the unequal grouping should be negligible. The variances for the yield traits in Table 6

are consistent with this conclusion since the top and bottom pairs of variances are not consistently greater than the intervening variances. Fat percentage is discussed in greater detail in section VII.

In order to assess the possibility of heterogeneity of variance, Bartlett's test (Snedecor, 1956) was used. The χ^2 of this test was significant for milk ($\chi^2 = 19.74$, $P \sim 0.05$, 11 d.f.), not significant at the 0.05 probability level for fat ($\chi^2 = 8.00$), and highly significant for fat percentage ($\chi^2 = 70.04$, $P < 0.01$, 11 d.f.). The heterogeneous variances for fat percentage increase with the mean and this is examined more closely in section VII. For the yield traits, the evidence is not conclusive as to the validity of the assumption of homogeneity of variance, but there do not seem to be regular relations between daughter variance and dam mean.

The only possible evidence found in the literature for change in phenotypic variance with level of production, independent of environment, was work reported in abstract form by Touchberry (1963). When 20,024 Holstein daughter-dam pairs were placed into 20 groups on (presumably dam) milk yield, each group with a range of 400 lbs. of milk, the within-herd dam and daughter phenotypic variances increased with level of production for milk yield, decreased with level of milk production for fat percentage, and increased for fat yield. In the present study the yield variances did not so increase. Since fat percentage is negatively correlated with milk yield the

decrease in variance for the former trait might mean an increase in variance with level of fat percentage, as found in the present study.

This work should not be confused with work showing change in variance with level of herd production. Reports reviewed by Van Vleck and Bradford (1964) for milk yield show that total variation increases with level of herd yield. Similar trends were found for milk and fat yield by Mitchell et al. (1961) and Van Vleck (1963), and for fat yield by Legates (1962).

Table 6. Variances of daughter records associated with fixed dam groups, in ascending order of dam mean yield

Milk Yield	Fat Yield	Fat Percentage
18.65	16.37	11.08
16.27	13.48	9.41
19.15	16.23	9.94
16.73	14.00	10.97
16.47	14.54	8.72
17.34	14.68	12.43
16.19	13.84	11.30
16.78	14.31	13.30
21.98	14.78	10.27
20.08	15.23	11.77
17.90	15.54	14.97
19.32	16.34	16.24

VII. TRANSFORMATION OF FAT PERCENTAGE

A. The Transformations

Since, of the three traits, the distribution of fat percentage deviation departed most from the normal, this trait was utilized in a consideration of various types of transformation that might be employed to make it more closely satisfy the assumptions of the analysis of variance. The expression of actual fat percentage, as well as fat percentage deviated from a mean, is such as to result in the distribution of the trait being skewed, as shown in section VI. The proportion of the higher values making up the tail of larger positive deviations is small however and the distribution has quite a narrow range giving the peaked form. It would seem that there is a lower limit to the content of fat in the milk below which it is rare to find examples, but that there are a number of "superior" animals with milk having fat percentages higher than expected under any hypothesis of a symmetric distribution. Von Krosigk (1959) and Gowen (1924) found similar skewed distributions for fat percentage.

It seems that the elimination of low testing cows is an important part of the voluntary selection of females in mid-western Holstein herds. This elimination of the lower end of the distribution in the preceding generation would tend to impart to first lactation records the type of skewed distribution found in these data.

The first type of transformation to try seemed logically to be one which would normalize the distribution of the trait. A procedure to find a transformed scale with the desired property was worked out as follows. The area midpoint of the frequency distribution was first found as that point having 50% of the observations to either side. This point fell almost on the midpoint of the group containing the mean, assuming a uniform distribution of observations within this group. Starting from this midpoint, the cumulative areas to each successive group midpoint in both the positive and negative directions were calculated, again assuming uniform distributions within each group. The values of abscissae in standard measure (t) corresponding to these areas were found from tables of the cumulative normal frequency distribution. These t values, when multiplied by the standard deviation (σ = 0.317), became scale values for the group midpoints in both positive and negative directions, starting from a central zero. Essentially the same type of transformation was derived by Cox (1962) for mortality in pigs at different ages.

The theoretical frequencies of observations falling in each group could have been obtained from the formula

$$\text{frequency} = \frac{\text{I. n. (ordinate)}}{\sigma}$$

where I is the group interval, n is the number of observations (n = 5209), and the ordinate is that of the normal curve for each

given value of t. Unfortunately it was not possible to determine values for I, but the use of approximate values enabled a check to be made on the method. The actual frequency distribution, the cumulative areas and the transformed scale are given in Table 7.

The mean fat percentage on the new scale was 0.000 while the standard deviation was 0.314, in line with that measured in the original percentage units. The g_1 and g_2 statistics were estimated as 0.00424 and 0.03060, with variances 0.00115 and 0.00460, respectively. As expected, neither statistic was significantly different from zero, indicating that the transformed data closely approached a normal distribution.

A skewed distribution with a positive tail can sometimes be made symmetric by a logarithmic transformation, or, less violently, by a square root transformation. These two transformations were the next to be tried. The 29 groups were given values from 1 to 29 and the natural logarithms and square roots of these values were obtained. The mean on the logarithmic scale was 2.458 with standard deviation 0.311, while the mean on the square root scale was 3.459 with standard deviation 0.510. The estimates of g_1 and g_2 on the logarithmic scale were -0.97673 and 3.56713 with variances 0.00115 and 0.00460, while the values for these estimates on the square root scale were -0.14747 and 0.87999 with variances 0.00115 and 0.00460, respectively. All four estimates were highly significant ($P<0.01$). The transformed distributions are extremely peaked and

Table 7. Results from the procedure to find a scale to normalize the distribution of fat percentage deviation

Group	Frequency distribution	% of observations in group	'Cumulative area	'Midpoints on new scale ($t\sigma$)
1	2	0.04	-49.98	-1.19
2	5	0.10	-49.91	-0.99
3	14	0.27	-49.73	-0.88
4	32	0.61	-49.29	-0.78
5	57	1.09	-48.44	-0.68
6	91	1.75	-47.02	-0.60
7	163	3.13	-44.58	-0.51
8	306	5.87	-40.08	-0.41
9	417	8.00	-33.14	-0.30
10	543	10.42	-23.93	-0.20
11	667	12.80	-12.32	-0.10
12	628	5.92 6.14	0.00	0.00
13	600	11.52	11.90	0.09
14	484	9.29	22.31	0.19
15	365	7.01	30.46	0.27
16	270	5.18	36.55	0.35
17	203	3.90	41.09	0.43
18	115	2.21	44.15	0.50
19	81	1.55	46.03	0.55
20	62	1.19	47.40	0.61
21	43	0.83	48.41	0.68
22	26	0.50	49.07	0.74
23	11	0.21	49.43	0.80
24	8	0.15	49.61	0.84
25	5	0.10	49.73	0.88
26	3	0.06	49.81	0.92
27	3	0.06	49.87	0.95
28	3	0.06	49.93	1.01
29	2	0.04	49.98	1.19

skewed, but now the excess of items is larger than the mean and the tail is to the left of the distribution. Both transformations have over-corrected the skewness and the logarithmic transformation, in particular, has violently reversed the skew and reinforced the peakedness.

In the previous section it was reported that the daughter variances for fat percentage deviations were heterogeneous and showed a tendency to increase with the dam mean. This is illustrated in Figure 4. An examination of Figure 4 led to the conclusion that linear regression fits the relation between variance and mean reasonably well. The variances for the bottom one and top two dam means could be biased upwards because of uneven group intervals as discussed in section VI, but it is believed that this bias is not large and that most of the extra variance associated with the upper two means is due to the tail of the distribution being concentrated in these two groups. Even were the three variances to be removed, there would still be a relation between variance and mean (Figure 4). The variances and means on the coded, additive scale are given in Table 8 (the daughter variances are the same as those in Table 6). The linear regression of daughter variance on dam mean was calculated and the coefficient found to be 0.4045 ± 0.1086. This value is significantly greater than zero ($P<0.01$, 10 d.f.). The regression line is drawn in Figure 4.

Bartlett (1947) and Kempthorne (1952) have suggested a way

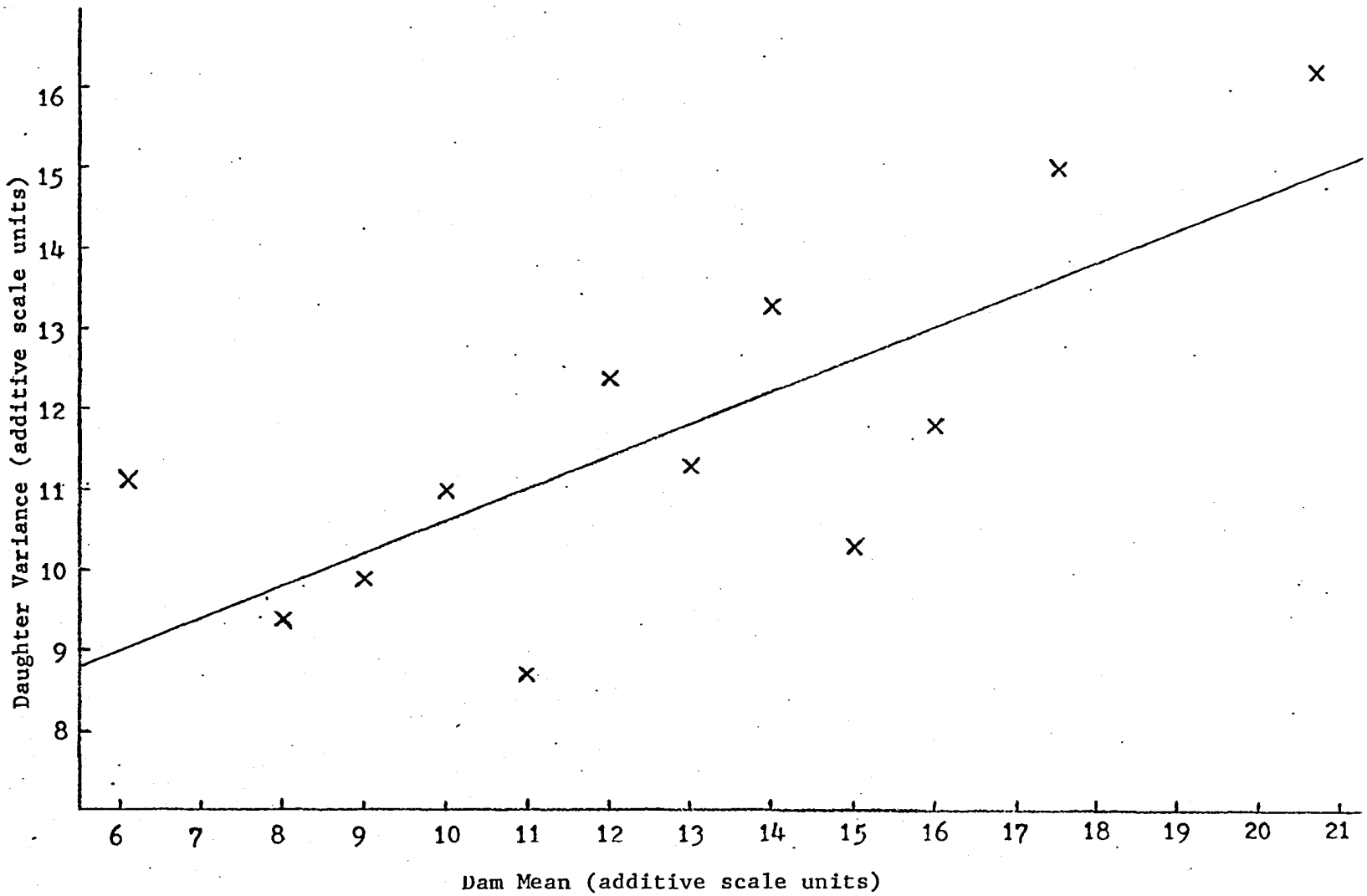

Figure 4. Linear regression of daughter variance on dam mean for fat percentage deviation

to utilize this type of relation in finding a transformation to make the error variances less heterogeneous. Their method is adapted for use in this case. Let t be the transformed variable, Y the daughter production, and X the dam production. A necessary restriction is that the transformed scale should be the same function of the original (additive) scale for both daughters and dams.

Thus, $t = g(X)$, $dt = g'(X)\,dx$, and $V(t) = (g'(X))^2 \cdot V(X)$,

where V(t) and V(X) are the respective variances.

But V(X) is approximately equal to V(Y).

Therefore $V(t) = (g'(X))^2 V(Y)$.

But it is known that $V(Y) = f(X) = (a + bX)$ from the linear regression relation between daughter variance and dam mean (Figure 4) where a is a constant (a = 6.566) and b is the linear regression coefficient (b = 0.4045).

Therefore $V(t) = (g'(X))^2 \cdot f(X)$.

But it is desired that V(t) should be constant.

Therefore,

$$(g'(X))^2 \cdot f(X) = C^2$$

and $C = g'(X) \cdot \sqrt{f(X)}$

But $g'(X) = dt/dx$

Therefore $C = dt/dx \cdot \sqrt{f(X)}$

and $t = \int \frac{C \cdot dx}{\sqrt{f(X)}}$

$$= C\int \frac{dx}{\sqrt{a + bX}} \qquad = \frac{2C}{b}\sqrt{a + bX}$$

$$= C' \sqrt{X + a/b} \qquad = C' \sqrt{X + 16.23}$$

Therefore, the approximate transformations for variables X and Y are $\sqrt{X + 16}$ and $\sqrt{Y + 16}$.

Von Krosigk (1959) derived a similar transformation for fat percentage using the relation between breed mean and the within-breed variance. In the present study, the daughter variances increased with the daughter means as well as with the dam means, as can be seen in Table 8. A transformation could have been worked out using this relation, but while stabilization of within-daughter-group variance with respect to group mean is desirable, the primary object of the present exercise was to stabilize the variance of the dependent variable with respect to levels of the independent variable in order to satisfy one of the assumptions of the linear regression analysis.

The effectiveness of the above transformation can be judged by examination of the daughter variances within dam groups calculated on the transformed scale and also presented in Table 8. There is no reason to reject the hypothesis that the variances are still heterogeneous since the χ^2 of Bartlett's test ($\chi^2 = 50.41$) is highly significant ($P<0.01$, 11 d.f.). However, the linear regression of daughter variance on dam mean now yields a regression coefficient of 0.0234 ± 0.0100, and while this value is significantly different from zero ($P<0.05$, 10 d.f.), it's size suggests that the linear

relation between variance and mean has been disrupted.

The mean daughter fat percentage on the transformed scale was 5.304 with standard deviation 0.329. $\hat{g}_1$ and $\hat{g}_2$ were 0.21495 and 0.48035 with variances 0.00115 and 0.00460 respectively. Both estimates are highly significant ($P<0.01$), the distribution being peaked and skewed like the original untransformed fat percentage distribution.

It was decided to attempt to find a transformation of the type $t = \sqrt{X + C}$, where C is a constant, which would remove the skewness from the fat percentage distribution. Trial and error yielded a transformation in which C was equal to three. The mean fat percentage on this transformed scale was 3.875 with standard deviation 0.452. Again, estimates of g_1 and g_2 were calculated and found to be 0.01020 and 0.67199 with variances 0.00115 and 0.00460 respectively. The latter was highly significant ($P<0.01$), but there was no reason to suppose the former to be different from zero, suggesting that the skewness had been removed.

Since, as mentioned in section II, heterogeneity of variance can be due to non-normality of the distributional property of the data, it was decided to examine the effect of the normalizing transformation (Table 7) on the relation between daughter variance and dam group mean. The daughter variances and dam means were calculated on the new scale and are presented in Table 8. There is again no reason to reject the hypothesis of heterogeneous variance

since the χ^2 of Bartlett's test ($\chi^2 = 27.81$) is highly significant ($P<0.01$, 11 d.f.). The coefficient of the linear regression of daughter variance on dam mean is now only 0.00825 ± 0.00795, and this value is not significantly different from zero at the 0.05 probability level. It appears that the normalizing transformation has been more effective in breaking up the relation between variance and mean than the transformation especially designed to do this task, ($\sqrt{X + 16}$), emphasizing the dependence of the relation on non-normality in the present case.

Table 8. Mean fat percentage deviations for groups of daughters and dams, and the corresponding daughter variances, on three different scales

Daughter Mean	Dam Mean	Daughter Variance	Dam Mean	Daughter Variance	Dam Mean	Daughter Variance
Coded additive scale			$t = \sqrt{X + 16}$		Normalizing scale	
10.54	6.12	11.08	4.70	0.103	-0.59	0.098
10.88	8.00	9.41	4.90	0.087	-0.41	0.084
11.36	9.00	9.94	5.00	0.091	-0.30	0.087
11.50	10.00	10.97	5.10	0.099	-0.20	0.094
11.80	11.00	8.72	5.20	0.076	-0.10	0.073
12.20	12.00	12.43	5.29	0.109	0.00	0.100
12.42	13.00	11.30	5.39	0.099	0.09	0.092
12.93	14.00	13.30	5.48	0.112	0.19	0.098
13.02	15.00	10.27	5.57	0.086	0.27	0.078
13.23	16.00	11.77	5.66	0.100	0.35	0.088
13.72	17.46	14.97	5.78	0.122	0.46	0.102
14.61	20.71	16.24	6.06	0.130	0.65	0.105

B. Regression of Offspring on Parent

Milk yield deviation, fat yield deviation, fat percentage deviation and the five transformations of fat percentage deviation were used in the regression analysis in order to estimate heritabilities and genetic correlations. The object of this analysis was to obtain some assessment of the effects of the transformations on the estimates of genetic parameters.

There seem to be two general classes of transformations which can be considered theoretically, both being members of a single, two-parameter family of transformation (Tukey, 1957; Moore and Tukey, 1954). The two classes are

(1) $t = (X + C)^p$ and

(2) $t = \ln (X + C)$

The first includes the various square root transformations and the second the logarithmic transformation of the present study.

For class (1), if Y is the daughter variable and X the dam variable,

$$t_Y = (Y + C)^p$$

and

$$t_X = (X + C)^p$$

$$dt_Y = p(Y + C)^{p-1}\, dY$$

and

$$dt_X = p(X + C)^{p-1}\, dX$$

Taking the first two terms of Taylor's series,

$$t_Y = t(\bar{Y}) + \frac{dt(Y)}{dY}\Big|_{Y=\bar{Y}} (Y - \bar{Y})$$

from which, $V(t_Y)$ is approximately equal to

$$\frac{p^2 (\bar{Y} + C)^{2p}}{(\bar{Y} + C)^2} V(Y)$$

Similarly,
$$V(t_X) = \frac{p^2 (\bar{X} + C)^{2p}}{(\bar{X} + C)^2} V(X)$$

and
$$Cov(t_X, t_Y) = p^2(\bar{X} + C)^{p-1}(\bar{Y} + C)^{p-1}Cov(X,Y)$$

where $\bar{X}$ and $\bar{Y}$ are the estimates of the means of X and Y respectively, V stands for variance and Cov for covariance. The regression of Y on X yields the regression coefficient,

$$b_t = \frac{Cov(t_X, t_Y)}{V(t_X)}$$

$$= \frac{p^2(\bar{X} + C)^{p-1}(\bar{Y} + C)^{p-1} Cov(X, Y)}{p^2(\bar{X} + C)^{2p-2} V(X)}$$

$$= \frac{(\bar{Y} + C)^{p-1}}{(\bar{X} + C)^{p-1}} \frac{Cov(X, Y)}{V(X)}$$

where $\frac{Cov(X, Y)}{V(X)}$ equals the regression coefficient from the untransformed variables. Doubling the regressions to obtain heritabilities,

$$h_t^2 = \frac{(\bar{Y} + C)^{p-1}}{(\bar{X} + C)^{p-1}} h^2 .$$

If $p = 1/2$, $\quad h_t^2 = \sqrt{\frac{(\bar{X} + C)}{(\bar{Y} + C)}}\ h^2$.

and if $\bar{X} = \bar{Y}$, $\quad h_t^2 = h^2$.

For class (2), with similar notation, $\quad t_X = \ln(X + C)$

and $\quad dt_X = (1/(X + C))\ dX$

similarly $\quad dt_Y = (1/(Y + C))\ dY$

$$\mathrm{Cov}(t_X, t_Y) = \frac{1}{(\bar{X} + C)(\bar{Y} + C)}\ \mathrm{Cov}(X,Y)$$

and $\quad V(t_X) = (1/(\bar{X} + C)^2)\ V(X)$

Therefore, $\quad b_t = \frac{(\bar{X} + C)}{(\bar{Y} + C)}\ \frac{\mathrm{Cov}(X,Y)}{V(X)}$

and $\quad h_t^2 = \frac{(\bar{X} + C)}{(\bar{Y} + C)}\ h^2$

again, if $\bar{X} = \bar{Y}$, $\quad h_t^2 = h^2$

If these theoretical derivations can be taken at their face value, little change in heritability should be expected from these general classes of transformation depending only on the daughter mean being approximately equal to the dam mean. The case of the normalizing transformation is a little more complicated since it applies specifically to the data from which it is derived and cannot be given a generalized treatment.

The results obtained from the regression analysis are given in Tables 9-11, the regressions being calculated within sire groups

using the 4,633 pairs with sire identification on the daughters. For milk and fat there were thirty groups and an additive scale from one to thirty, while for fat percentage and the transformations there were twenty-nine groups. The grouping was the same as that described in section VI, except that the records falling off the ends of the range were included in the end groups.

The offspring means and variances are a little less than the parental estimates, an effect also found among the ungrouped data and reported in Table 3. The estimates of heritability and genetic correlation are similar to the corresponding estimates calculated in the within-sires analysis of section V.A, showing that the grouping has little effect on the estimation. The standard errors of the genetic correlation coefficients would also be of the same order as those reported in Table 5.

The regression coefficients and heritability estimates for the various measures of fat percentage deviation are ranked in descending order of magnitude. It so happens that this order is the same as would be found were the measures to be ranked in increasing order of magnitude of the disruption of the scale from a purely additive scheme. The possibility therefore exists that the more disruptive the transformation, the lower the heritability of the transformed trait, although the differences are very small. The genetic correlations between fat percentage and each of the transformations are close to unity, but again there are trends in the correlations of each of the

additive scaled traits with the fat percentage traits. These trends will be referred to further in section IX but, although they exist, the differences between the estimates of heritability are so small that they cannot be considered of significance since the most extreme values differ only by the magnitude of a standard error.

Table 9. Means, standard deviations of observations and regression coefficients for the three deviation traits and transformations of fat percentage deviation, from the within-sire regression of daughter on dam

	Parent		Offspring		Regression
	Mean	Std. Dev.	Mean	Std. Dev.	Coefficient**
Milk	16.71	4.19	15.80	4.13	0.1756 ± 0.01896
Fat	16.87	3.72	16.01	3.73	0.1737 ± 0.01932
Fat Percentage (X)	12.25	3.36	12.22	3.18	0.2753 ± 0.1775
$\sqrt{X + 16}$	5.31	0.31	5.30	0.30	0.2752 ± 0.01786
Normal (X)	0.00	0.30	0.00	0.29	0.2748 ± 0.01786
$\sqrt{X + 3}$	3.88	0.43	3.87	0.41	0.2735 ± 0.01798
$\sqrt{X}$	3.46	0.48	3.46	0.47	0.2714 ± 0.01807
ln X	2.46	0.29	2.46	0.28	0.2564 ± 0.01861

**All regressions highly significant ($P < 0.01$, 2611 df.).

Table 10. Heritability estimates from within-sire regression of daughter on dam for milk, fat, fat percentage and various transformations of fat percentage deviation

Trait	Heritability estimate
Milk	0.351 ± 0.038
Fat	0.347 ± 0.039
Fat Percentage (X)	0.551 ± 0.035
$\sqrt{X + 16}$	0.550 ± 0.036
Normal X	0.550 ± 0.036
$\sqrt{X + 3}$	0.547 ± 0.036
$\sqrt{X}$	0.543 ± 0.036
ln X	0.513 ± 0.037

Table 11. Genetic correlations among milk, fat and fat percentage deviations and the various transformations of fat percentage deviation

Milk X Fat			0.811	
Milk X Fat Percentage (X)			-0.359	
Fat X Fat Percentage			0.249	
		Milk	Fat	Fat Percentage
$\sqrt{X + 16}$	X	-0.355	0.252	1.000
Normal X	X	-0.351	0.257	0.998
$\sqrt{X + 3}$	X	-0.351	0.258	0.999
$\sqrt{X}$	X	-0.348	0.261	0.998
ln X	X	-0.333	0.274	0.992

VIII. MAXIMIZATION OF HERITABILITY

A. The Maximization Procedure

As mentioned in the introductory section on criteria for biological scales, a valuable procedure might be to find for a trait the scale on which the genetic gain expected from mass selection is maximized. A method to find such a scale, in which the heritability of a trait as calculated from the resemblance between parent and offspring is maximized, was developed by Rae (1950). Rae used the method to assign values to subjective grades of fleece quality in sheep, the values found being those that maximized the regression of daughter on dam. Five hundred and forty-seven daughter-dam pairs were used and the regression coefficient found was compared with one calculated after assigning values starting at zero and increasing by equal steps of 0.125 to unity. The method was tried in the present study on the much more extensive data available for the three lactation traits, the data being grouped so that values could be assigned to the midpoints of the groups.

A more comprehensive outline of the method than is given by Rae (1950) follows:

Let the midpoints of the dam groups be given the values t_1, t_2, ..., t_p progressively and let the corresponding midpoints of the daughter groups be given the same values. The daughter values (t_i) are the values of the dependent variable and the dam values (t_j)

those of the independent variable.

With this type of two way classification, the sum of products of deviations from the mean is given by

$$\sum_{ij} n_{ij} t_i t_j - \frac{(\sum_i n_{i\cdot} t_i)(\sum_j n_{\cdot j} t_j)}{n_{\cdot\cdot}} ,$$

where i and j equal 1, 2, ..., p,

n_{ij} is the number of observations in the ith daughter and jth dam group,

and the · signifies summation over the appropriate subscript.

The sum of squares of midpoint values for dams is given by

$$\sum_j n_{\cdot j} t_j^2 - \frac{(\sum_j n_{\cdot j} t_j)^2}{n_{\cdot\cdot}}$$

When the regression is calculated within-sires as described in section V, the sum of products and sum of squares are given by

$$\sum_{ij} n_{ij\cdot} t_i t_j - \sum_k \left[\frac{(\sum_i n_{i\cdot k} t_i)(\sum_j n_{\cdot jk} t_j)}{n_{\cdot\cdot k}} \right]$$

and

$$\sum_j n_{\cdot j\cdot} t_j^2 - \sum_k \left[\frac{(\sum_j n_{\cdot jk} t_j)^2}{n_{\cdot\cdot k}} \right]$$

where k signifies a sire group and equals 1, 2, ..., s. Let the sum of products be designated by P and the sum of squares by S. The sample regression coefficient, $b = \frac{P}{S}$.

To maximize b with respect to any t_i, P/S is differentiated with

respect to t_i and the derivative set equal to zero. This gives a set of p equations of the form

$$\frac{\partial b}{\partial t_i} = \frac{S\frac{\partial P}{\partial t_i} - P\frac{\partial S}{\partial t_i}}{S^2} = 0$$

and these equations can be put in the following form:

$$\frac{\partial P}{\partial t_i} - b\frac{\partial S}{\partial t_i} = 0 \qquad (1)$$

For b to be a maximum, it is sufficient that the matrix of second derivatives of b with respect to the t_i be negative definite. It was not found possible to prove this true analytically in a general form. The second order partial derivatives of b can be written out and evaluated for sign, the evaluation ultimately depending upon the sign of $(P_{ii}S - S_{ii}P)$ or $(P_{ij}S - S_{ij}P)$ where P_{ii}, P_{ij}, S_{ii} and S_{ij} are as defined below. An examination of the actual values of these terms for all i and j and for each of the traits in the present study, showed that $S_{ii}P$ was always greater than $P_{ii}S$ but that $S_{ij}P$ was not necessarily greater than $P_{ij}S$. This does not demonstrate conclusively the presence of a negative definite form, but the method and later results suggest that b is in fact maximized.

By factoring the $t_i t_j$ terms from P and S,

$$P = P_{11}t_1^2 + P_{12}t_1t_2 + \ldots + P_{1p}t_1t_p + P_{21}t_2t_1 + P_{22}t_2^2 + \ldots + P_{pp}t_p^2$$

and $$S = S_{11}t_1^2 + S_{12}t_1t_2 + \ldots + S_{1p}t_1t_p + S_{21}t_2t_1 + S_{22}t_2^2 + \ldots + S_{pp}t_p^2$$

Thus $$\frac{\partial P}{\partial t_i} = 2P_{ii}t_i + \sum_{\substack{j \\ j \neq i}} P_{ij}t_j$$

and $$\frac{\partial S}{\partial t_i} = 2S_{ii}t_i + \sum_{\substack{j \\ j \neq i}} S_{ij}t_j$$

where $$P_{ii} = n_{ii\cdot} - \sum_k \frac{n_{i\cdot k}n_{\cdot ik}}{n_{\cdot\cdot k}}$$

$$P_{ij} = n_{ij\cdot} + n_{ji\cdot} - \sum_k \frac{n_{i\cdot k}n_{\cdot jk} + n_{j\cdot k}n_{\cdot ik}}{n_{\cdot\cdot k}}, \quad i \neq j$$

$$S_{ii} = n_{\cdot i\cdot} - \sum_k \frac{n_{\cdot ik}^2}{n_{\cdot\cdot k}}$$

and $$S_{ij} = -2\sum_k \frac{n_{\cdot ik}n_{\cdot jk}}{n_{\cdot\cdot k}}, \quad i \neq j$$

Substituting for $\frac{\partial P}{\partial t_i}$ and $\frac{\partial S}{\partial t_i}$ in equation (1), the following set of simultaneous equations emerges:

$$\begin{aligned} &2P_{11}t_1 + P_{12}t_2 + \ldots + P_{1p}t_p - b(2S_{11}t_1 + S_{12}t_2 + \ldots + S_{1p}t_p) = 0 \\ &\vdots \\ &P_{p1}t_1 + P_{p2}t_2 + \ldots + 2P_{pp}t_p - b(S_{p1}t_1 + S_{p2}t_2 + \ldots + 2S_{pp}t_p) = 0 \end{aligned}$$

Vector 1 Vector 2

Vector 1 can be factored into a square, symmetric matrix (C) and a vector (T). Similarly, vector 2 can be factored into a matrix (Q) and the same vector (T). T is the vector of t values.

This gives

$$(C - bQ)T = 0 \qquad (2)$$

where 0 is the zero vector. The elements of the matrices C and Q sum to zero over any row or any column, the row and column vectors are linearly dependent, and the matrices are singular from the nature of their formation. The set of equations can be made of full rank by placing one restriction upon the number of t values. Setting t_1 equal to zero removes the first column from each matrix. Since each remaining row vector can be expressed as a linear combination of the other row vectors in the same matrix, any row can be removed. It seems convenient to remove the first row and column from C and Q giving reduced matrices E and R.

Equation (2) can now be expressed as

$$(E - bR)U = 0 \qquad (3)$$

where U is the reduced vector of t values.

Since R has an inverse,

$$(R^{-1}E - bI)U = 0 \qquad (4)$$

where I is the identity matrix. Let $R^{-1}E = A$.

This system of homogeneous, linear equations has a solution for U, if and only if Determinant (A-bI) = 0.

Det (A-bI) = 0 is the characteristic equation of A and,

on expansion, yields a polynomial in b of degree p-1. The largest characteristic root of this polynomial is the desired maximum value of the regression coefficient, b. For another example of this use of determinants consider the generation matrix theory of inbreeding as given by Kempthorne (1957).

The corresponding characteristic vector is a solution for U of equation (4). A unique solution can be found by standardizing the vector in some way or, alternatively, by putting the solution for b into equations (3) or (4), setting U_{p-1} equal to some constant, removing an arbitrary row of the matrix to make the system of full rank, and solving for the p-2 values of U.

The following iterative process for determining the largest characteristic root of a matrix A and the corresponding characteristic vector is an application of the method given by Aitken (1937) and used by Rae(1950) to find his largest root.

Let b_1 be the largest root of the square (but not necessarily symmetric) matrix A. b_1 is a real root, all b_i are distinct and $|b_1| > |b_i|$ for all i = 2, 3, ..., p-1.

Let Y_o be an arbitrary p-1 rowed, non-zero vector, e.g. a vector of ones.

The following sequence is formed.

$$Y_{i+1} = AY_i , \quad i = 0, 1, 2, \ldots$$

There exist constants $C_1, C_2, \ldots, C_{p-1}$ such that

$$Y_o = C_1X_1 + C_2X_2 + \ldots + C_{p-1}X_{p-1}$$

where the X_i are the characteristic vectors of A. X_1 corresponds to U of equation (4) when b_1 corresponds to b.

Then

$$Y_1 = AY_o = C_1AX_1 + C_2AX_2 + \ldots + C_{p-1}AX_{p-1}$$

But AX = bX by definition.

Therefore, $Y_1 = C_1b_1X_1 + C_2b_2X_2 + \ldots + C_{p-1}b_{p-1}X_{p-1}$

and $Y_{k+1} = C_1b_1^{k+1}X_1 + C_2b_2^{k+1}X_2 + \ldots + C_{p-1}b_{p-1}^{k+1}X_{p-1}$

Since $|b_1| > |b_i|$, $i \neq 1$, then $b_1 \neq 0$

and $$\frac{Y_{k+1}}{b_1^{k+1}} = C_1X_1 + \frac{C_2b_2^{k+1}X_2}{b_1^{k+1}} + \ldots + \frac{C_{p-1}b_{p-1}^{k+1}X_{p-1}}{b_1^{k+1}}$$

Now $\left|b_i/b_1\right| < 1$ for $i \neq 1$

and limit
$k \longrightarrow \infty$ $\left|b_i^{k+1} \Big/ b_1^{k+1}\right| \longrightarrow 0$

Assuming $C_1 \neq 0$ by initial choice of Y_o,

$$\lim_{k \longrightarrow \infty} \frac{Y_{k+1}}{b_1^{k+1}} = C_1X_1$$

From which can be obtained the required vector U.

But it is necessary to have b_1.

$$\lim_{k \longrightarrow \infty} \frac{Y_{k+1}}{Y_k} = \frac{C_1b_1^{k+1}X_1}{C_1b_1^{k}X_1} = b_1$$

and this is true for each element of Y_{k+1} divided by Y_k at the limit.

In other words, each vector Y divided by the previous vector yields estimates of b_1 which converge to a constant value when k is large. It is recommended that k be larger than the dimension of A (Aitken, 1937).

B. The Determination of the New Scales

The C and Q matrices were computed in the first instance on the basis of 30 groups for daughters and dams, the grouping being made as in section VI. This was done for milk and fat deviations only. When the reduced matrix R was found for milk, it's determinant was to all intents and purposes zero. This was still the case when the first three rows and columns were removed. A few numerical examples served to show that the removal of a row and column in such a matrix does not remove the singularity if the row and column are substantially zero vectors, caused by any n_i being equal to zero. An inspection of the Q matrix for milk revealed very small numbers in the first three rows, most of the entries being zeros. In the case of the Q matrix for fat, the first two rows were zero vectors. It was concluded that this factor was causing the continued singularity in the R matrices. It might have been possible to continue the operation in the case of milk, since the determinant was not quite zero (an inverse was found), but the fat case was impossible.

The decision was therefore made to reduce the number of groups, in order to have smaller matrices with more cells filled in the marginal rows and columns. The new grouping was into twenty groups each way with the following ranges and group intervals;

Milk Yield from -6600 lbs. to +7000 lbs. by 680 lbs,

Fat Yield from -220 lbs. to +260 lbs. by 24 lbs,

Fat Percentage from -0.7% to +1.1% by 0.09%.

For milk yield, 4,558 daughter-dam pairs were included in this range, distributed within 1,011 sire groups. The C and Q matrices were computed and the reduced R matrix successfully inverted. The largest characteristic root of the matrix $(R^{-1}E)$ was then found by the iterative process outlined. Good convergence was obtained with k equal to 20 and the value of the root so found was 0.180624. A solution for the vector U was then attempted by replacing b in the equation

$$(E - bR)U = 0$$

with the above value for the largest root, setting U_{19} equal to 19, removing the last row of (E-bR), and solving for the remaining 18 values of U. These solutions are values for $t_2,\ldots,t_{19}$ and are given in Table 12. The solutions are in the reverse order to that expected when it is remembered that t_1 equals zero and t_{20} equals 19.

As a check on the method, a solution was also attempted by operations identical to those above except that the equation

$$(R^{-1}E - bI)U = 0$$

was used. These solutions are also given in Table 12. The solutions from both of the above methods are supposed to be unique and identical because t_{20} was set equal to 19 in both cases. However, if the numbers of daughter-dam pairs in the end groups are small, the values assigned to these groups (t_1 and t_{20}) may have little influence on the solutions to the sets of equations. If this is true, then setting t_1 equal to zero merely removes the data in the bottom class from further consid-

Table 12. Scale values which maximize heritability of milk yield deviation, found by solving two different sets of simultaneous equations

	Solutions from $(E - bR)U = 0$	Solutions from (column (a)) (-0.1)	Solutions from $(R^{-1} E - bI)U = 0$
	(a)	(b)	(c)
t_2	195.8	-19.58	-19.79
t_3	366.6	-36.66	-37.24
t_4	174.7	-17.47	-17.96
t_5	263.2	-26.32	-26.31
t_6	213.6	-21.36	-22.38
t_7	218.8	-21.88	-21.03
t_8	120.4	-12.04	-13.66
t_9	98.2	- 9.82	-10.97
t_{10}	84.6	- 8.46	- 9.75
t_{11}	95.3	- 9.53	-11.01
t_{12}	8.4	- 0.84	- 3.34
t_{13}	-25.8	2.58	0.01
t_{14}	-17.8	1.78	- 0.87
t_{15}	-50.3	5.03	2.27
t_{16}	-111.2	11.12	7.69
t_{17}	-196.4	19.64	15.43
t_{18}	-127.9	12.79	7.96
t_{19}	-315.5	31.55	14.28

eration rather than fixing the lower end of the scale at zero. Similarly, setting t_{20} equal to 19 does not ensure a predetermined unique solution but merely enables a solution to be found. Consequently, the solutions in each case are only one of an infinity of solutions that could have been found, and multiplying these solutions by a constant still satisfies the equation. The solutions from (E - bR), multiplied by -0.1, given in the second column of Table 12, are comparable with the solutions from (R^{-1} E - bI).

For fat yield, 4,537 daughter-dam pairs were included in the range. The corresponding number for fat percentage was 4,556. Again, C and Q matrices were computed and the R matrices inverted. The largest roots of the (R^{-1} E) matrices were found, this time with k equal to 30, although reasonable convergence had been obtained by the time k reached 20. The values obtained were 0.187994 for fat and 0.283025 for fat percentage. Solutions for the vector U were attempted by the second method utilized above for milk yield, that is, by solving the equation

$$(R^{-1} E - bI)U = 0$$

In each case the results obtained were useless from the point of view of using the scales in subsequent work. The 18 values for both traits were grouped around zero with a range of from -4.20 to +2.55 for fat and from -1.32 to +1.19 for fat percentage and there were no consistent trends in direction. After attempting an additional restriction for fat percentage ($t_2 = 0$) and a different restriction for fat yield ($t_{11} = 10$ instead of $t_{20} = 19$), both to no avail, it was decided to abandon this approach. It had been hoped in the latter

case that fixing a value in the middle of the range might yield a more useful unique solution than fixing the upper end value, but it seems that the nature of the problem is such that fixing any one single value does not necessarily yield the desired type of scale.

It was decided to return to the iterative process which had been used to determine the largest characteristic root of $(R^{-1} E)$ for each trait and use the process to find the corresponding characteristic vector, which should be one of the infinity of solutions for vector U. If any one of these solutions is used in daughter-dam regression analysis, the same maximized regression coefficient should result since each solution is a linear function of each other solution. For all three traits, the process was continued until k equalled 30. For milk yield, the resulting vector was multiplied by the factor found to make the last value (t_{20}) equal to 19. Because there seemed to be something peculiar about the last value for fat yield, the vector was multiplied by the factor necessary to make the second to last value (t_{19}) equal to 18. The vector for fat percentage was handled like that for milk yield. The resulting scales are given in Table 13 and these scales are the ones used in all subsequent analyses.

In all three cases, t_1 equals zero, but only in the case of fat percentage does this seem to make sense. Consequently, in subsequent plotting and the correlation analyses below, t_1 was not included in the milk and fat yield data. In a similar way, t_{20} for fat yield was omitted from the graph and correlation analysis. However, all scale

Table 13. Scale values which maximize heritabilities of milk, fat and fat percentage deviation, found from the characteristic vectors associated with the largest characteristic roots

	milk yield	fat yield	fat percentage
t_1	0.00	0.00	0.00
t_2	-19.78	-7.58	2.01
t_3	-37.24	-4.60	5.66
t_4	-17.96	-4.46	5.58
t_5	-26.31	-2.50	6.17
t_6	-22.38	0.62	7.17
t_7	-21.03	0.55	9.03
t_8	-13.66	2.45	9.15
t_9	-10.97	2.29	10.22
t_{10}	- 9.75	4.02	11.57
t_{11}	-11.01	3.95	12.51
t_{12}	- 3.34	5.73	13.08
t_{13}	0.01	7.05	15.30
t_{14}	- 0.87	8.65	15.48
t_{15}	2.27	7.63	14.02
t_{16}	7.69	12.13	15.57
t_{17}	15.43	13.92	17.32
t_{18}	7.96	14.46	14.56
t_{19}	14.28	18.00	17.86
t_{20}	19.00	6.69	19.00

values were used in the daughter-dam regression analyses of section VIII C. The first point to note is that the scale for milk is identical with that found by solving the equation $(R^{-1} E - bI) U = 0$, (see Table 12) as it should be mathematically. The three new scales of Table 13 were compared with a strictly additive scale running from + 1 to + 20. The relations between the new scales and the additive scale are plotted in Figures 5, 6, and 7. The correlations between the new and additive scales are 0.956 for milk yield, 0.986 for fat yield, and 0.981 for fat percentage, while the linear regressions of new scale on additive scale are

milk yield	2.637 ± 0.198	(17 df)
fat yield	1.314 ± 0.056	(16 df)
fat percentage	0.911 ± 0.043	(18 df)

The above statistics suggest that the scale obtained for fat percentage conforms most closely to the additive scale. However, when allowance is made for the change in the spread of the scales, all three conform closely to an additive pattern with the scale for milk yield deviating most from a strictly linear relation. It is perhaps not surprising that the trait (fat percentage deviation) with the closest relation between daughters and dams (and therefore the highest heritability) should give a scale most closely fitting to an additive scale, but further discussion on this point will be reserved for later.

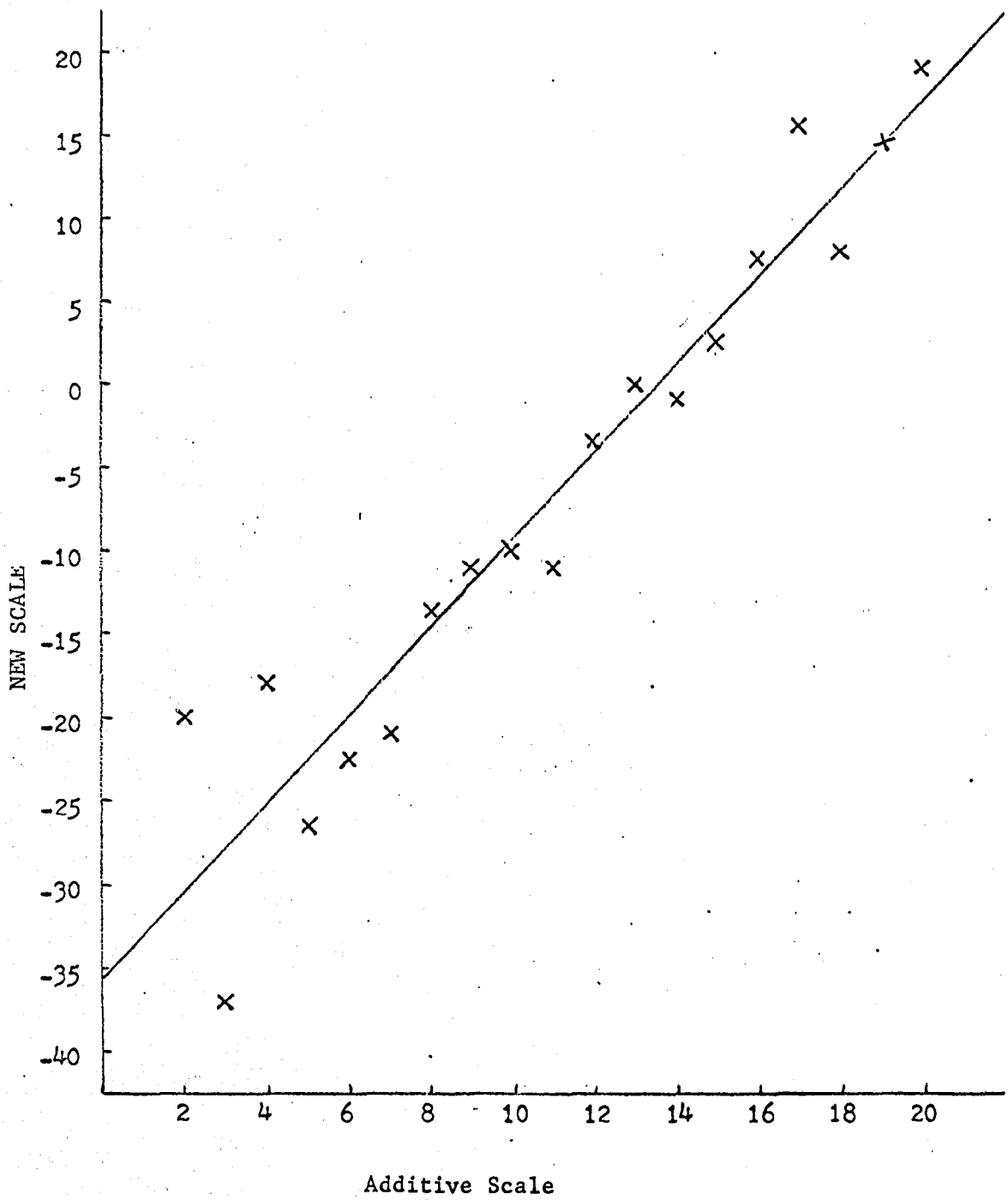

Figure 5. Linear regression of scale values from the maximization procedure on additive scale values for milk yield deviation

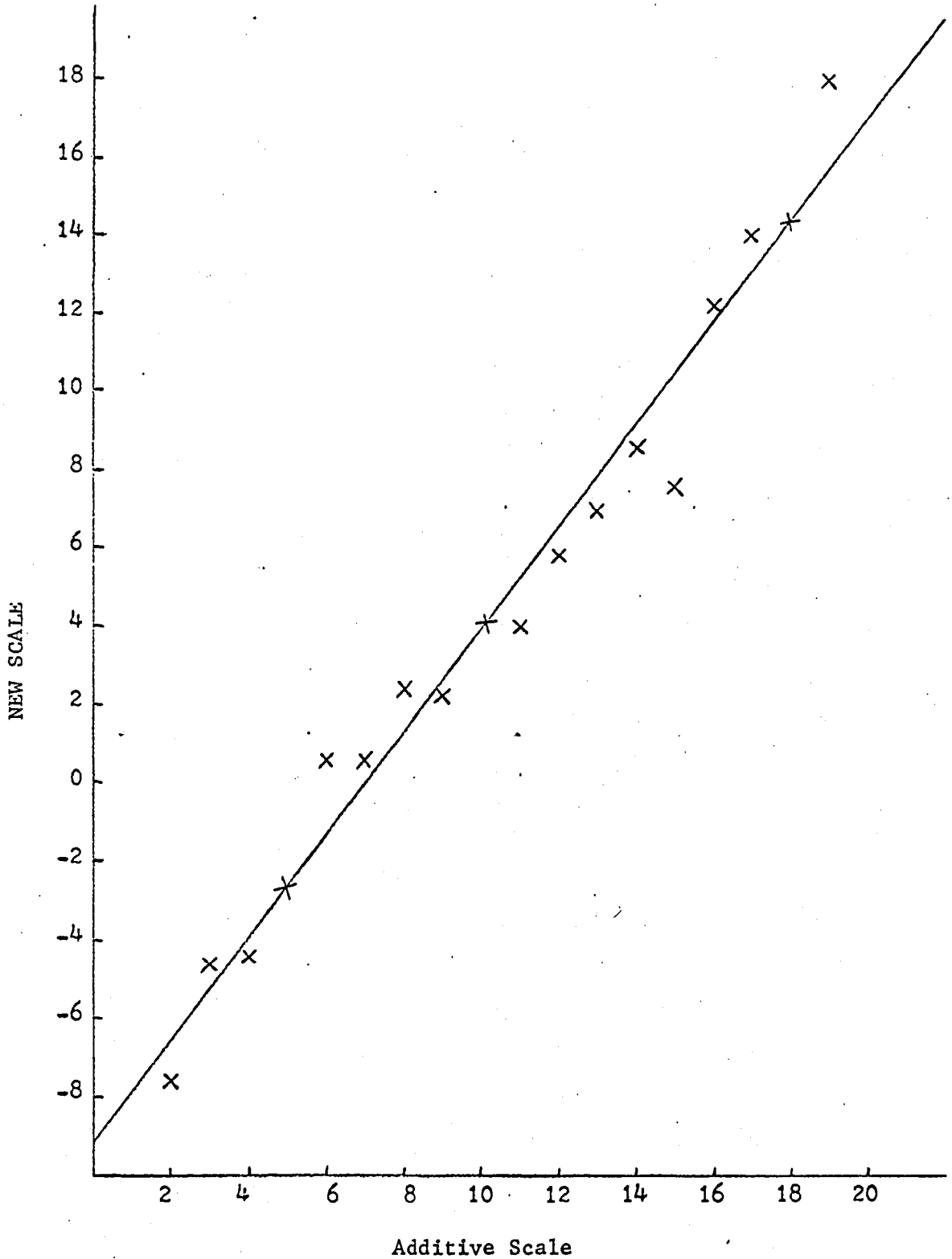

Figure 6. Linear regression of scale values from the maximization procedure on additive scale values for fat yield deviation

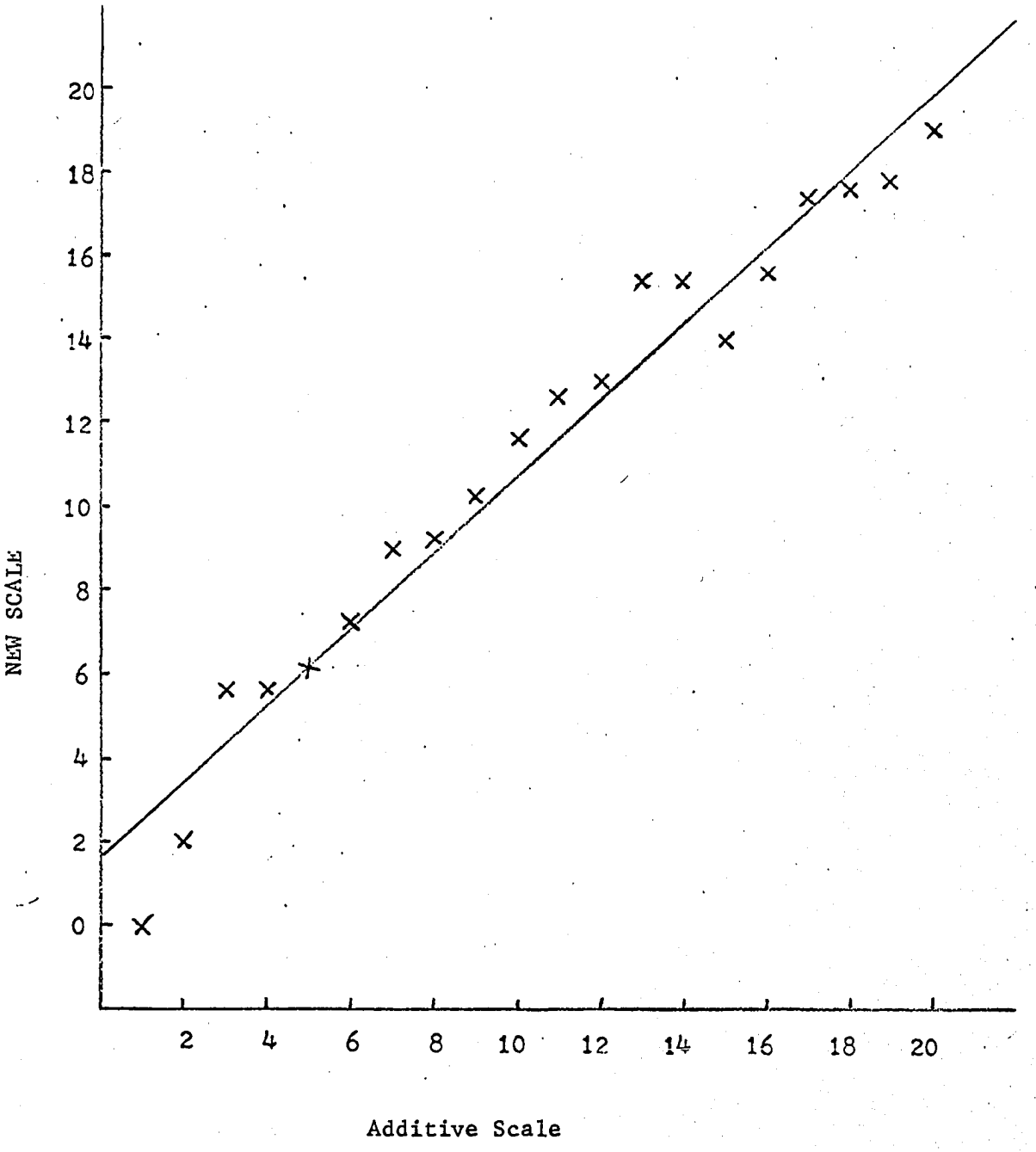

Figure 7. Linear regression of scale values from the maximization procedure on additive scale values for fat percentage deviation

C. Regression of Offspring on Parent

Daughter-dam regressions were calculated for the three traits using an additive scale (20 values from + 1 to + 20) and the scales derived by maximizing the daughter-dam regression coefficients (Table 13). There were 4,558 pairs for milk yield, 4,537 pairs for fat yield and 4,556 pairs for fat percentage deviation. The regressions were calculated within sire groups as before. Mean values for daughters and dams for the three traits each measured on two scales are given in Table 14, along with the corresponding standard deviations. As in the case of the ungrouped data of Table 3, offspring means are less than parental means and offspring variances generally less than parental variances, but again not by any great margin. The standard deviation for milk yield deviation on the new scale (that which maximizes the heritability) is large compared with that on the additive scale. The reason is to be found in the range of values in the new scale for milk yield as shown in Table 13.

The regression coefficients are given in Table 15. Only those regressions having the same trait and same scale for each variate are used to estimate heritabilities. The remaining coefficients are used in the estimation of genetic correlations, either between traits or between the two measures of the same trait. Comparisons of the regressions having both variates on an additive scale with those from the ungrouped data (Table 4) show the effect of consolidating the data into twenty groups.

Since the object of the re-scaling was to maximize the within-sire heritability estimates for each of the traits, the maximized estimates are set out in Table 16 along with those calculated using the additive scale. These can be compared with the original within-sire estimates in Table 5. There has been a slight reduction in the sizes of the estimates on an additive scale due to the grouping process and a very slight increase in the standard errors. The maximized estimates are, in all cases, larger than the original estimates, but there is little change in the variances of these estimates. The regression coefficients from which the maximized heritabilities are derived should be identical to the largest characteristic roots found and used in the derivation of the new scales. In the cases of fat yield and fat percentage there is perfect identity, but in the case of milk yield there is a discrepancy, due it is believed to rounding during the computations. The value derived from regression analysis is the one used below.

The actual increases in heritability in Table 16 are 0.018 for milk, 0.032 for fat, and 0.020 for fat percentage. The differences on a regression coefficient basis were tested and yielded "t" values of 0.333, 0.568 and 0.394, all non-significant with degrees of freedom 5072, 5030 and 5068 for milk, fat and fat percentage respectively.

The new scales have already been compared with the additive scales by means of phenotypic correlation and linear regression. The within-sire regression analysis yielded estimates of the genetic correlations among the three traits as measured on both sets of scales. The cor-

relations between the two measures of the same trait were 1.006 for milk, 0.997 for fat, and 0.997 for fat percentage, and these values are very close to unity (rounding error probably accounts for the value greater than unity). The remaining genetic correlations are given in Table 17 and there do not seem to be any consistent trends or peculiarities in these estimates. The standard errors of all of these estimates of genetic correlation will be small and of the same order as those calculated previously and reported in Table 5.

Table 14. Means and standard deviations of observations for milk, fat and fat percentage deviation, each measured on an additive scale and on a scale designed to maximize heritability

	Parent		Offspring	
	Mean	Std. Deviation	Mean	Std. Deviation
Additive Scale				
Milk	11.14	3.26	10.46	3.23
Fat	10.88	3.25	10.20	3.27
Fat Percentage	8.91	3.25	8.88	3.05
New Scale (Table 13)				
Milk	-6.79	9.23	-8.66	9.14
Fat	4.76	3.84	4.01	3.83
Fat Percentage	10.24	3.08	10.21	2.98

Table 15. Regression coefficients and standard errors from within-sire regression of daughter on dam, using additive scales and scales designed to maximize heritabilities

		Parental trait, Additive Scale		
Offspring trait		Milk	Fat	Fat percent.
Additive Scale	Milk	0.1740 ± 0.01938	0.1401 ± 0.01962	-0.0708 ± 0.02000
	Fat	0.1323 ± 0.02008	0.1722 ± 0.01977	0.0523 ± 0.02035*
	Fat Percent.	-0.0799 ± 0.01880	0.0505 ± 0.01891	0.2729 ± 0.01781
New Scale	Milk	0.4944 ± 0.05475	0.4068 ± 0.05580	-0.2249 ± 0.05651
	Fat	0.1665 ± 0.02345	0.2136 ± 0.02309	0.0625 ± 0.02376
	Fat Percent.	-0.0795 ± 0.01832	0.0483 ± 0.01851	0.2662 ± 0.01741

*Coefficient significantly greater than zero ($P<0.05$). All other coefficients highly significant ($P<0.01$)

Table 15. (Continued)

	Offspring trait	Parental trait, New Scale: Milk	Fat	Fat percent.
Additive Scale	Milk	0.0653 ± 0.00684	0.1224 ± 0.01663	-0.0779 ± 0.02111
	Fat	0.0509 ± 0.00709	0.1508 ± 0.01674	0.0537 ± 0.02148*
	Fat Percent.	-0.0253 ± 0.00666	0.0432 ± 0.01600	0.2884 ± 0.01880
New Scale	Milk	0.1831 ± 0.01931	0.3557 ± 0.04730	-0.2430 ± 0.05970
	Fat	0.0628 ± 0.00827	0.1880 ± 0.01954	0.0642 ± 0.02508*
	Fat Percent.	-0.0248 ± 0.00647	0.0410 ± 0.01565	0.2830 ± 0.01836

*Coefficient significantly greater than zero ($P<0.05$). All other coefficients highly significant ($P<0.01$)

Table 16. Maximized heritability estimates and estimates from grouped daughter-dam pairs (additive scale) for milk, fat and fat percentage deviation

	Additive Scale	Maximizing Scale
Milk	0.348 ± 0.039	0.366 ± 0.039
Fat	0.344 ± 0.039	0.376 ± 0.039
Fat Percentage	0.546 ± 0.036	0.566 ± 0.037

Table 17. Genetic correlations among milk, fat and fat percentage deviation each measured on an additive scale and on a scale designed to maximize heritability

Scale Combination	Trait Combination		
	Milk X Fat	Milk X Fat Percentage	Fat X Fat Percentage
Additive X Additive	0.787	-0.345	0.237
Additive X New	0.789	-0.355	0.231
New X Additive	0.810	-0.338	0.229
New X New	0.806	-0.341	0.222

IX. DISCUSSION

The foregoing analyses enable a consideration to be made of the effects of grouping of data on estimations of parameters, in terms of loss of information. When the records were consolidated into thirty groups (twenty-nine for fat percentage), the means and standard deviations were estimated very close to those from the ungrouped records. With the traits measured on additive scales, estimates of heritabilities and genetic correlations were also very similar from the grouped and ungrouped data. The effect of consolidation of milk yield deviation, fat yield deviation and fat percentage deviation records into twenty groups, still using additive scales, was to lower very slightly the heritabilities and positive genetic correlations and similarly raise the negative genetic correlation. The variances of the heritability estimates from the grouped data were a little higher, but so little that it can be concluded that there is no loss of information after such grouping, which is analogous to severe rounding.

The main objective of the analyses was to investigate the effects of transformations of scale on estimations of heritability and genetic correlation. Four regular transformations and one empirical transformation of fat percentage, a trait with a non-normal distribution being peaked and slightly skewed, were tried. Theoretical study led to the suggestion that the effects should not be great and this was confirmed in practice. Changes in the estimates as a result of scale changes were minimal and are not considered sufficient to make any

practical differences in applied breeding programs in the near future.

The estimates (Table 10) show that the further the transformed scale departs from a purely additive scheme, the lower the heritability. Lush (1954) has suggested that if the phenotypic scale is far from linear with the scale of the actual effects of the genes, the heritability is under-estimated. The above then is evidence for the possibility that the genotypic scale for fat percentage is largely additive. The genetic correlations with milk and fat yields (Table 11) also changed progressively with increasing disruption of the additive scale, the former negative correlation decreasing and the latter positive correlation increasing. There are notable similarities between the two sets of correlations involving the transformations which remove the skewness from the distribution of fat percentage. It was thought that scales giving symmetry to the data might yield higher estimates of heritability but simple numerical examples soon show that this is not automatically true. It appears that, at least for fat percentage, the additive scale is optimal and this is perhaps fortunate since this scale is most convenient and gives results that are comparatively easy to interpret and use.

Since a transformation makes the same changes in each variate it is not difficult to envisage why little change occurs when heritability is estimated by regression techniques. For genetic correlations, the coefficient is a function of the harmonic mean of two regressions which tend to be altered in opposite directions, thus again giving the expectation of little change in the statistic.

Empirical scales were derived (Table 13) on which the heritabilities of the three production traits were maximized. The changes observed in the heritability estimates were in the positive direction, but they were small. The improvement expected from mass selection is sensitive to change in heritability, but not sensitive enough for the changes found here to make any practical differences, especially in view of the error inherent in using these estimates with data other than that from which they were derived, and in view of the general inaccuracies in current predictive procedure. The optimum breeding structure of a population is even less sensitive to changes in heritability (Legates, 1962).

Genetic gain per generation is a simple function of heritability and the selection differential. The gain predicted in this way will be on the same scale as the selection differential, and the heritability should have been estimated from data on this scale. Since the scales found by the maximization procedure, as well as that found to normalize the distribution of fat percentage deviation, are a consequence of the data and methods, they are not expected to be constant but to vary like heritability. For this reason, the scales might not be easy to use in the generalized prediction necessary to evaluate breeding plans.

Again, therefore, it is perhaps fortunate for the sake of convenience that additive scales appear to be practically as useful as scales specifically designed to maximize heritability. Stated in another way, there are no losses in utility when the latter scales

are considered additive. Such additivity means that phenotypic units of measurement of the trait are of equal value along the scale. The lack of substantial changes in the estimates of heritability after re-scaling, and the additivity of the new scales, suggest that the genotypic scales for all three traits are largely additive. This probably means that the amounts of non-additive genetic variance and interaction variance removable from the total phenotypic variance by re-scaling are small.

It might be worthwhile to speculate about the likelihood of having achieved worthwhile increases in heritability by changes of scale in these traits. Two types of evidence might be of assistance, the first being the presence or absence of genotype X environment interactions, and the second being the presence or absence of curvilinearity of the regression of daughter on dam.

Genotype X environment interaction, of either of types A or B according to the classification of McBride (1958), might be removable by scaling. Type A involves intra-population genotypes X micro-environments while type B involves the same genotypes X macro-environments. These interactions, if present, are carried along with, or are like the error term in the deviations of records from herd-year-season averages and in the expectations derived therefrom. They most likely cause inflation of the denominator of the heritability ratio, thus lowering the estimate below what it might be if such sources of error could be removed. Kelleher (1964) has reviewed the pertinent literature on bull X herd and bull X herd-year-season interactions in dairy cattle.

The review, and his own work, led him to the conclusion that such interactions (of type B) are of minor importance, as might be expected in dairy data when the range of environments and genotypes is comparatively small. McBride (1958) points out that there is no direct evidence as to whether type A interactions (involving the local environment of each individual cow) exist or not, and their absence is usually assumed. There is no evidence as to whether or not they could be important enough to cause fluctuations in the phenotypic scale giving maximum expression to heritability.

Non-linearity of the regression of genotype on phenotype may be an indication of non-additivity in either or both of the genotypic and phenotypic scales. Beardsley et al. (1950) tried to fit a curve to the daughter-dam relation for fat yield within breed, sire and herd. Curvilinear regression did not differ significantly from linear regression, but did fit the data more closely, the trend being for decreasing heritability with increasing dam production. The problem can be considered in terms of change in heritability with change in genotypic level, expressed in terms of individual phenotype. Using milk yield deviations from herd-year-season averages, Bradford and Van Vleck (1964) found no trend in the heritability from daughter-dam regression with increasing dam yield. Touchberry (1963), using within-herd daughter-dam regression, found a decrease in the heritability of fat yield with increasing dam milk yield, but no such trend for the heritability of milk yield. The heritability of fat percentage increased with level of milk production, and since fat percentage is negatively correlated with milk yield, this heritability could have decreased with level of fat percentage.

It appears, therefore, that there is a possibility that the heritabilities of fat yield and fat percentage decrease with production increase, giving curvilinearity that could be due to interaction or non-additivity in the scales. Any such effects however did not show up in the present study.

The trait with the highest heritability, fat percentage, had the best fit of it's maximizing scale to additivity. This trait also had, by a small margin, the lowest standard error of estimate of heritability (Table 16). Since the data from such a trait has the best fit to the linear regression model, there is less chance to increase the estimate by alterations to the phenotypic scale. Transformations of scale to maximize heritability did not result in a lowering of the sampling variances of the estimates for any of the traits however, presumably because there were no large changes in the scales. It is suggested that valuable changes in the regressions of daughter on dam from the maximizing procedure are unlikely when the structure of the data is similar in both generations. Greater changes might be expected in the scales, in the heritabilities or in the variances of the estimates when the trait is such that the daughter and dam distributions are irregular or the calculated regression has a large sampling variance. Such traits are likely to be, although not necessarily, those with low heritability and to have the possibility of much non-additive variance which might be removable by scaling.

A method could perhaps be evolved to maximize the genetic correlation between two traits with different distributions, but this

would require a different approach to the one used here. In the present study, changes in the genetic correlations are secondary to changes in heritability.

With regular known transformations, theory and practice suggest that for most traits, little improvement in heritability is likely from manipulation of scales. There is no clear way to obtain similar theoretical evidence for empirical transformations, but the results make it reasonable to suggest that these act in a similar way. Perhaps if the means of distributions were very different in the generations of daughters and dams some advantages might be gained from transformations but this seems unlikely to be often encountered in regular livestock data. The general conclusion is that for the traits used in this study, no real gains in livestock improvement from selection can be expected by attempting to maximize heritability, alter the scales from additivity, normalize the distribution of the trait, or transform the scale to make the data more closely fit the assumptions of analysis of variance. There might be other reasons for trying to make the data fit the assumptions and, if this is the case, and transformations of scale are used to do it, it can be said that the procedure is unlikely to cause too much upset to predictions of genetic gain by altering appreciably the estimates of genetic parameters.

X. SUMMARY

There is a fundamental relation between the phenotypic scale on which a production trait in livestock is measured and the practical value which can be placed upon estimates of genetic parameters and consequent breeding plans. The effects of several transformations of scale on estimates of heritability of three production traits in dairy cattle and the genetic correlations among these traits are considered in this study. Within-sire estimates of heritability of first lactation milk yield, fat yield and fat percentage, each expressed as deviations from contemporary herd-mate averages, and the genetic correlations among these traits, were computed using 4,633 pairs of daughters and their dams. The estimates found are consistent with estimates reported by other workers using similar data and are used as a reference base for the study of transformation of scale. The heritabilities estimated were 0.353, 0.345 and 0.556 for milk, fat and fat percentage respectively while the genetic correlations were 0.815 between milk and fat, -0.330 between milk and fat percentage, and 0.265 between fat and fat percentage.

The daughter deviation records were combined into 29 or 30 groups and the frequency distributions of the three traits were studied. Milk and fat are close to normally distributed while fat percentage is peaked and slightly skewed with the tail of observations to the upper end of the distribution. Consequently this latter trait was chosen to study transformations that would normalize the distri-

bution of the trait, make the distribution symmetric, and break up a relation which was found between daughter variance and dam mean.

An empirical transformation to normalize the distribution was derived. Other transformations studied were ln X, $\sqrt{X}$ and $\sqrt{X+3}$, the last being found to make the distribution symmetric. A positive linear relation between daughter variance and dam group mean was found to be disrupted by a transformation of the form $\sqrt{X+16}$ as well as by the normalizing transformation. A theoretical derivation based on an approximation involving Taylor's series, led to the suggestion that little change in heritability should be expected after regular transformations, provided that the daughter mean is approximately equal to the dam mean. This suggestion was supported in practice when the above five transformations were used in within-sire regression analyses. The changes in heritabilities and genetic correlations were minimal.

A procedure to find a phenotypic scale which leads to a maximization of the regression of daughter on dam(and thus heritability) was utilized for each of the three production traits. The scales found were linearly related to a strictly additive scale and were themselves substantially additive. The procedure yielded heritability estimates of 0.366, 0.376 and 0.566 for milk, fat and fat percentage respectively, and genetic correlations of 0.806 between milk and fat, -0.341 between milk and fat percentage, and 0.222 between fat and fat percentage. The differences between the maximized heritabilities and those calculated using additive scales were all positive but very small, being less than the standard error of either

estimate.

The general conclusion is that for these production traits in dairy cattle (and most probably for the majority of production traits in livestock), no gains in heritability and therefore in livestock improvement can be made by manipulations of the phenotypic scale. It appears that additive scales are optimal, but if it is necessary to make a transformation of scale in order, for example, to make the data fit the assumptions of the analysis, such a change of scale is unlikely to alter greatly the estimates of heritability and genetic correlation obtained from the regression of offspring on parent.

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